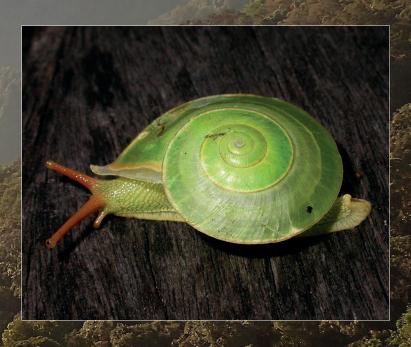
Land snails and slugs of Sabah and Labuan (Malaysia)

J.J. Vermeulen & T.-S. Liew



Institute for Tropical Biology and Conservation
Universiti Malaysia Sabah

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J J Vermeulen & T-S Liew (With contributions of M Z Khalik)



Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah

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LAYOUT, DESIGN AND TYPE SETTING: K. Anker & J.J. Vermeulen

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Preface

The history of the present handbook goes back to the first years of this century. During the early days of the BOR/MOL collection (Mollusca collection of Universiti Malaysia Sabah), material of land snails appeared difficult to identify. Literature on Sabah snails was generally scarce, scattered over mainly 19th century publications, and covered only a part of the species present in the material.

To address this problem, the first author started a manuscript with a concise overview over the Sabah snail fauna, which would finally develop into this handbook. The first unpublished version started circulating among Sabah students of the snail fauna around 2002. It covered all snail families, but while some are shortly revised, others are no more than an uncritical list of species names. Unidentified species were listed with numbers (e.g. 'Charopa sp. 2'), or with codes ('Charopa sp. BO-02'), or with unpublished species names ('Charopa infrastriata', without a valid description following ICZN rules). A new, more extensive but still unpublished version of the manuscript appeared in 2006. The informal species names (i.e. nomina nuda) increasingly posed a problem because they were used in publications by students of the Bornean snail fauna. Also, the many shortcomings of the manuscript directly translated into misidentifications in those publications. This made the production and publication of the present, more carefully considered handbook a matter of urgency. Having said that, the authors in no way claim that this work is more than a step on the long road leading to a representative knowledge of the land snail fauna of Sabah.

The production of this handbook had the 2006 version of the unpublished manuscript as a starting point, together with the revision of key groups in Vermeulen et al. 2015, as well as revisions of various other groups, some up-to-date, others with a slight patina of time. Together, these provided enough of a framework to complete the present handbook within a limited period.

Acknowledgements

A generous grant from the Lady McNeice Foundation to Universiti Malaysia Sabah (GLA0014-2018) made possible the last and crucial phase of this project: Revising the last groups of Sabah land snails that had escaped attention until then, and the assemblage of all information to this handbook. We thank Ms. Shelagh Tonkin for making the necessary arrangements.

We thank Universiti Malaysia Sabah for support in many ways: Grant management, administration, use of research facilities such as the scanning electron microscope, logistic support during field work. The material in BOR/MOL, on which much of this work is based, was collected with research grants awarded by Universiti Malaysia Sabah, by the Ministry of Higher Education of Malaysia, by the industry, and by NGO's.

We are also grateful for the permissions given by Sabah Biodiversity Centre, Sabah Parks, Sabah Forestry Department, Sabah Wildlife Department, Sabah Foundation, and many district offices to carry out research in the protected areas and forest reserves over the past 20 years, and to join many scientific expeditions organized by these agencies.

Han Raven allowed us the use of photographs of three species of maritime assimineids; Mohd Zacaery Khalik the use of SEM-images of *Georissa* species.

Before publication, this work was subjected to the scrutiny of three reviewers, Thierry Backeljau, Tan Siong Kiat and Barna Páll-Gergely. The authors are grateful for their meticulous work and valuable comments. However, all opinions expressed in the work are the authors'.

Introduction

Snail collecting in Sabah

The diverse nature of the Sabah land snail fauna remained largely unknown for a long time. Nineteenth century collectors only scratched the surface, and virtually no collecting was done in the first half of the 20th century. Sabah (and in fact the whole of Borneo) was largely left out of a spate of collecting activities and publications from the thirties to the sixties elsewhere in southeast Asia. Only three small papers on the Sabah snail fauna appeared: Solem 1964, Van Benthem Jutting 1966, and Saul 1967, the latter including a narrative of an excursion through leech-infested forest to Gomantong cave.

The large-scale collecting effort that provided the material for this handbook started in 1986, when the first author, while in Borneo to gather data for taxonomic work on orchids, as a collateral took large soil samples of every limestone hill he encountered during his travels. After more collecting in Kalimantan and Sarawak around 1990, his revisions of the sometimes spectacularly shaped Bornean Diplommatinidae highlighted the special nature of the Bornean snail fauna (Vermeulen 1991, 1993, 1994, 1996).

Around the start of the new millennium, these publications contributed to the decision to choose snails as one of the preferred subjects of study at Institute for Tropical Biology and Conservation (ITBC), Universiti Malaysia Sabah (UMS). The ITBC started the BORNEENSIS biodiversity collection. This included the Mollusca collection BOR/MOL, initiated by Menno Schilthuizen when he joined ITBC in 2000. The first entries were reference specimens donated by the first author and Wim Maassen. Between 2000 and 2006, undergraduate students expanded the collection with material collected throughout Sabah, under the supervision of Menno Schilthuizen.

At first, limestone areas got all the attention because of their conspicuously species-rich and easily sampled snail faunas. A few half-hearted and rather fruitless attempts, earlier, of the first author to find faunas elsewhere as rich and diverse as on limestone hills reinforced this bias and led to a short-lived assumption that the collections representatively covered the Sabah snail fauna. However, there were reports on species endemic to forests on sandstone/shale and granodiorite bedrock on mount Kinabalu (Tillier et al. 1988).

Therefore, the second author, as one of Menno Schilthuizen's students, undertook extensive surveys in several hitherto neglected environments on non-calcareous bedrock for his undergraduate and postgraduate studies between 2004 and 2007. He sampled montane forests in the Crocker Range, on Mount Tambuyukon and on Mount Kinabalu. Densities of individuals proved extremely low, but the collected material held a true treasure of unknown snail species. He also sampled offshore islands at Semporna and found a fauna including *Chloraea puella* and *Obba marginata*, elements of the Sulu archipelago fauna which on Sabah territory only occur just a few kilometers offshore the Bornean mainland.

Later, similar collecting efforts in other non-limestone areas in Sabah, often with an unusual geological underground such as serpentinite, yielded more interesting species. At present, aware as we are that snails may hide in small corners everywhere in the dwindling Sabah forests, we would rather not venture a guess how much of the Sabah snail fauna this handbook (including 343 species and subspecies) covers.

In 2006, Liew Thor-Seng took over the management of the BORNEENSIS land snail collection from Menno Schilthuizen, until he joined ITBC in 2008. While this year marked the end of all transfer of material between BORNEENSIS and foreign collections because of new, prohibitive state legislation, it was also the start of the taxonomic exploitation of the collections which, benefitting from earlier transfers, resulted in revisions of various snail groups (Schilthuizen and Liew 2008; Liew et al. 2009; Vermeulen et al. 2015). These revisions made possible the production of the present handbook.

This handbook

The handbook includes several snail groups that did not yet receive the attention that they deserve. For convenience, 'snails' is used as a collective noun throughout to include slugs and semi-slugs unless specifically stated.

For instance, the treatment of species included in Helicarionidae is patched together from very incomplete information. Sabah species of the genus *Helicarion* are only known from a few empty shells; in contrast, species of the genus *Sabalimax* are known from excellent descriptions of their anatomy ... but we know little about their shells.

Ariophantid semi-slugs are another example. Their revision suffers from general under-sampling of this group,

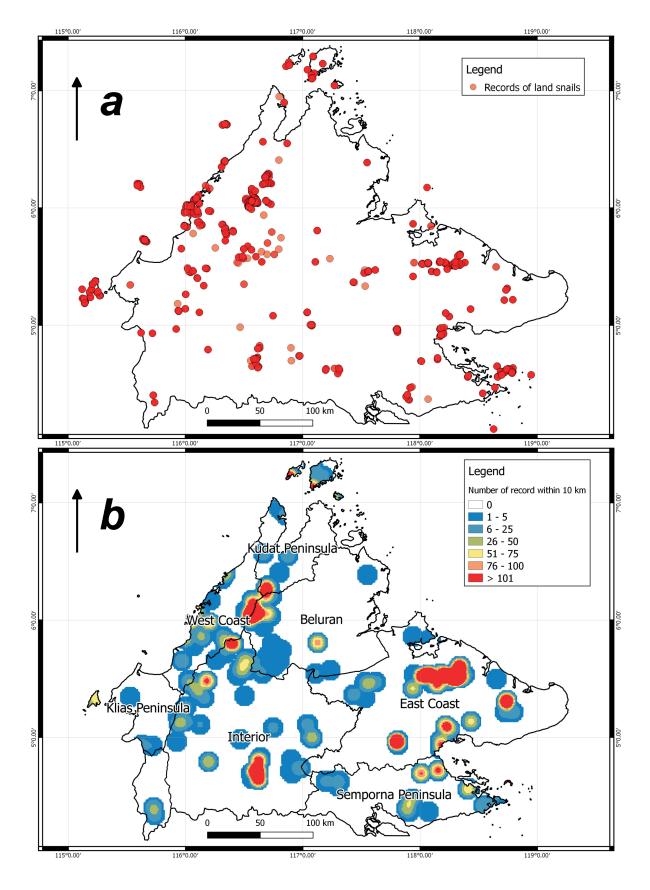


Fig. 1, a. Sampling sites since 1986, based on records in BOR/MOL and collection JV; b. Record density: the number of records within a 10 km radius of a location. Limestone areas and highlands over 1000 m score highest. Note that colours indicating numbers of records do not extend over sea, so that small but well-sampled islands remain invisible

INTRODUCTION

because collecting and processing soil samples, for a long time the preferred method of sampling, leads to their under-representation. It is also a challenge to match information from 19th and early 20th century literature, based on corroded, rubbery specimens in liquid preservation, which usually have a lead-grey color, with the often vividly colored little creatures we encounter in the forest. Prospective students, whom we advise to carefully photograph the animals they collect before reducing them to pickled specimens suitable for anatomical investigation and DNA research, will probably find much to comment upon in our work.

Rathouisiid slugs are arguably the least-studied land gastropod family in Asia. Species have been distinguished mainly by external features and colors. An unidentified rathouisiid slug in the Kinabatangan river valley is a predator of the operculate land snail *Plectostoma* sp. The evolutionary response of *Plectostoma* sp. to this predation has led to interesting theories on predator-driven evolution (Schilthuizen et al. 2006) ... but the rathouisiid slug remained unnamed. Here, this species is concisely described (*Atopos rapax* new species). Unfortunately, we had to rely on minimal preserved material since we were unable to find better material for a more extensive description, with our last attempt to obtain specimens being thwarted by the covid-19 pandemic. Bornean Rathouisiidae are truly in need of a taxonomic overhaul; we have seen photographs of rather similar-looking but almost certainly different animals from Kalimantan Timur, the Sabah highlands and Singapore (Tan et al. 2009).

Material

Our main sources of information are two extensive collections of Sabah land snails: The BORNEENSIS collections ('BOR/MOL', 9904 records) of Universiti Malaysia Sabah, gathered between 2000 and 2020, and the private collection of Vermeulen ('JV', 2063 records), collected between 1986 and 2005. The results of these collecting efforts are given in fig. 1a, showing all sampling sites. However, fig. 1b is more informative: It shows the number of records per sampling site. If combined with fig. 7, 8, and 9, it appears that areas on limestone bedrock, coastal areas, and highlands above 1000 m above sea level are richest in numbers of individuals. Land snails seem relatively scarce elsewhere but as said above, hills on volcanic soil or on serpentinite bedrock may be home to interesting species assemblages including narrow endemics.

We studied some specimens, or photographs of specimens, from other sources:

FMNH: Field Museum of Natural History, Chicago, Illinois, USA.

HNHM: Hungarian Natural History Museum, Budapest, Hungary.

HR: private collection J G M Raven, Wassenaar, the Netherlands.

KK: private collection of K Kittel, Wiesthal, Germany.

MZU: Zoology Museum, Universiti Malaysia Sarawak, Malaysia.

NHMUK: Natural History Museum, London, UK.

NMW: National Museum Wales, Cardiff, UK.

NNM: Nationaal Natuurhistorisch Museum, Naturalis, Leiden, The Netherlands.

SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany.

SP: Sabah Parks Museum, Sabah, Malaysia.

UF: Florida Museum of Natural History, Gainesville, Florida, USA.

VK: private collection V Kessner, Adelaide River, Australia.

ZMA: Zoological Museum Amsterdam, the Netherlands (now stored in NNM).

How to use this handbook

With this handbook, snails can be identified in two ways.

The first is by following a hierarchical system of binary identification keys (to units at higher taxonomic levels and to informal groups in larger genera) and cross diagnoses (usually with species) which work in tandem and together provide a diagnostic difference between each random couple of Sabah snail species. Starting with the 'Keys to the families', and following the leads, one ends up at a genus, or a species group within a genus. Cross diagnoses with the species should lead to a name for the snail to identify.

However, even the most hardened taxonomist cannot always resist the temptation to try and identify a snail by simply leafing through the pages and comparing it with illustrations. To facilitate this, we have added identification charts, fig. 10 to 13, with images of representative genera of all families of Sabah land snails. The user compares a snail with the images and checks out the families or genera with the most similar snails. However, this approach rather easily leads the user to the wrong families.

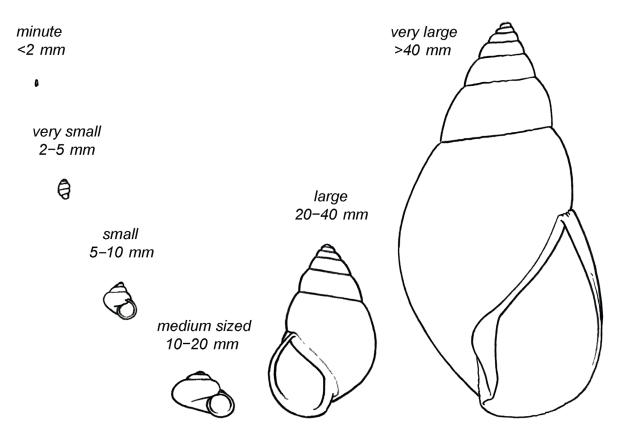


Fig. 2. Shell size categories

Both ways work best if used on living, adult (see note 3 with the keys to the families) snails. They need to be alive because only then the presence or absence of an operculum (see fig. 4) can be established, and they need to be adult because only then the animals show all characters needed for identification. It is sometimes difficult to reliably identify juveniles. Comparing them with adult specimens of the same species will yield results but caution is advised, particularly if adults and juveniles are not from the same location.

Information given with the species

Eventually, the keys or the identification charts lead the user to a group of species descriptions. Each species treatment starts with the accepted name and references to illustrations. After the accepted name follows:

Synonymy and literature

All synonyms pertaining to the same type specimen(s) (ICZN: Objective synonyms) are gathered in a single paragraph and sorted chronologically, with the original combination first. If a paragraph includes the accepted combination, the reference to the accepted combination is given first.

For each species, we cite all literature referring to material from Borneo. We also cite most pre-1900 literature, and at least one source summarizing the fauna of each of the surrounding areas: Peninsular Malaysia, Sumatra, Java, Bali and Sulawesi. If useful for a proper understanding of a species, we cite other literature.

Cross diagnoses

Cross diagnoses compare species with other species found in Sabah. If a species needs to be compared with others not found in Sabah, this information is provided below the species description, under the heading 'Similar species elsewhere'.

Species descriptions

Species descriptions are presented following the following format:

Shell [categorized size, see fig. 2, to give a first impression], [translucency], [color].

Surface [shiny/dull].

Spire [shape].

Whorls [convexity, profile; including the basal part of the shell].

Sculpture protoconch [radial sculpture, spiral sculpture]; teleoconch [radial sculpture, spiral sculpture].

Aperture [shape], [aperture teeth or lamellae].

Peristome [simple/double], [shape].

Umbilicus [open/closed].

Dimensions [height and width of the shell, ratio height divided by width], [diameters of the first three or four whorls], [number of whorls], [diameter umbilicus if open, ratio umbilicus diameter divided by shell diameter], [height and width of the aperture]; see fig. 5 and 6.

Operculum.

Periostracum.

External characters of living animal.

Anatomy.

Students of the Sabah fauna may find this model useful when preparing species descriptions. It would ensure an optimal fit of their work in the taxonomic framework provided here. They also could copy a description of a species resembling the one they wish to describe and modify the text where necessary.

We describe variability in shapes of shells, etc. in a concise way – often using brackets and n-dashes – that may need explanation. We give the following examples:

Spire ellipsoid to cylindrical = Spire varying between ellipsoid and cylindrical.

Spire ellipsoid-cylindrical = Spire intermediate between ellipsoid and cylindrical (resembles a cylinder that slightly tapers towards the end).

Spire (ellipsoid-)cylindrical = Spire varying between cylindrical and ellipsoid-cylindrical.

Spire ovoid(-cylindrical) = Spire varying between ovoid and ovoid-cylindrical.

Spire (ellipsoid-)obovoid to (cylindrical-)obovoid = Spire varying between ellipsoid-obovoid and obovoid, and between cylindrical-obovoid and obovoid (implying also a variation ranging from ellipsoid-obovoid to cylindrical-obovoid).

When describing variability in size we also use brackets, for example:

Shell height (5.1-)6.2-8.0 mm = Shell height usually between 6.2 and 8.0 mm, but a few specimens are smaller, down to 5.1 mm high.

Throughout the text, we use specific terminology which is explained in fig. 3 and 4. Measuring shells also follows specifications: Height and width of spire and aperture are measured along lines parallel to or perpendicular to the coiling axis of the spire (fig. 5). The diameters of the first three whorls are measured on adult shells, along the sutures, not on juveniles of 1, 2 or 3 whorls respectively. The difference is that in many species the upper side of the whorls are attached above the periphery (fig. 5).

Snails of the family Diplommatinidae are measured in a slightly different way, because the highly variable width of the peristome needs to be excluded from measurements to obtain relevant results; see fig. 6.

In some cases, anatomical features are needed to identify species, especially of the genitalia. For information about the morphology and functioning of land snail genitalia we refer to Gómez (2001), which is available online.

Terminology

We use some terminology and abbreviations that may need explanation:

antrorse = directed or pointing forwards (in the coiling direction of the spire and pointing away from the apex)

callus = a thickened part

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crescent-shaped = the shape of the moon during its first or fourth quarter phase
deciduous = easily falling or peeling off (for instance hairs, periostracum)
ellipsoid = like ovoid, but with the widest part half-way along the longest axis (3-dimensional)
elliptic = like ovate, but with the widest part half-way along the longest axis (2-dimensional)
erose = with a notched edge
foveolate = with very small, shallow pits
granulose = having the surface roughened with minute, rounded protrusions
N.P. = National Park
oblique to = inclined: Neither perpendicular nor parallel to (a plane, a line)
obliquely (conical) = a symmetrical shape (for instance a cone) without its axis of symmetry, because this
    is not perpendicular to base of the shape
obovate = a shape with the outline of an inverted egg (the narrow end pointing downwards) (2-dimen-
obovoid = inverted egg-shaped (the narrow end pointing downwards) (3-dimensional)
orthocline = growth lines or radial sculpture in a plane parallel to the coiling axis of the spire
ovate = a shape with the outline of an egg (2-dimensional)
ovoid = egg-shaped (3-dimensional)
nucleus = the central part of the operculum, where it started to grow
periostracum = a chitinous, usually transparent, brownish layer covering the outside surface of the shell
prosocline = growth lines or radial sculpture in a plane slanting forward with respect to the coiling axis
    of the spire
reniform = kidney-shaped
retrorse = directed or pointing backwards (in the coiling direction of the spire and pointing towards the
    apex)
rimate = shaped like a fissure or a cleft
rugose = a surface covered with wrinkles
rugulose = a surface covered with fine wrinkles
semi-(elliptic) = prefix meaning 'half', indicating that a part has an outline, for instance 'elliptic', cut in
    two halves
```

Distribution in Sabah

Terms indicating frequency of occurrence are 'rare' (1 to 4 localities), 'scattered localities' (5 to 10 localities), 'rather common' (11 to 20 localities), 'common' (more than 20 localities). However, we apply them in a somewhat loose fashion: A species occurring locally in a dense cluster of half a dozen localities but elsewhere on two localities only still qualifies as rare, although we may add a note on its local abundance. Only with rare species we provide localities.

Most of our material originates either from areas on limestone bedrock, or from coastal areas, or from land above 1000 m above sea level. Geographical entities in each of these categories are given on maps.

Fig. 7a shows limestone areas with their names as used in the text. Quite often, species are restricted to limestone hills in one or a few river valleys, see fig. 7b.

We use the term 'highlands' for land above 1000 m above sea level; see fig. 8a for the topographical units.

Larger topographical units used, particularly for lowland species, are found in fig. 8b.

The numerous islands along the coasts of Sabah are shown in fig. 9.

Quite frequently, we use the compass points, N, E, S, or W to indicate parts of Sabah, which is self-explanatory with the note that, again, the terms are loosely used.

Elevation range and environmental information

Elevation range and environmental information are compiled from information on the labels with the samples. Despite our considerable collecting efforts of the last four decades (fig. 1), the text may still reflect an incomplete

INTRODUCTION

dataset (insufficient sampling, limited information with the samples) rather than anything else in some cases.

Distribution beyond Sabah

The distribution in Borneo is based on records in literature and on samples in our collections; the distribution elsewhere is largely based on records in literature.

Similar species elsewhere

Some species (particularly new species) need to be compared with others not found in Sabah.

Variability

In some species which show more than average variability, we distinguish informal (meaning that we do not name them following ICZN) taxonomic units, e.g. in *Everettia subconsul*.

Notes

All other information on a species which does not fit any of the above headings finds a place here.

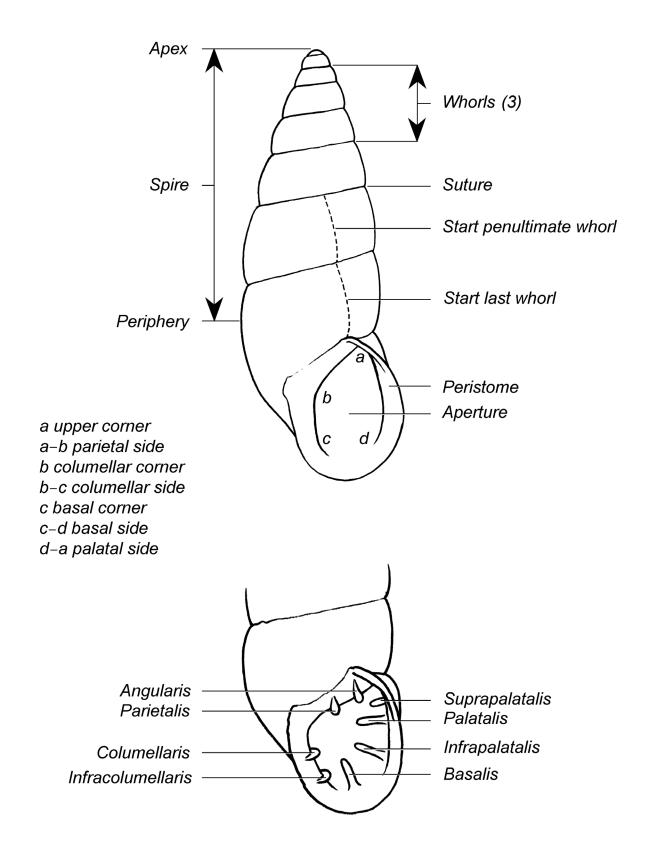


Fig. 3. Terminology.

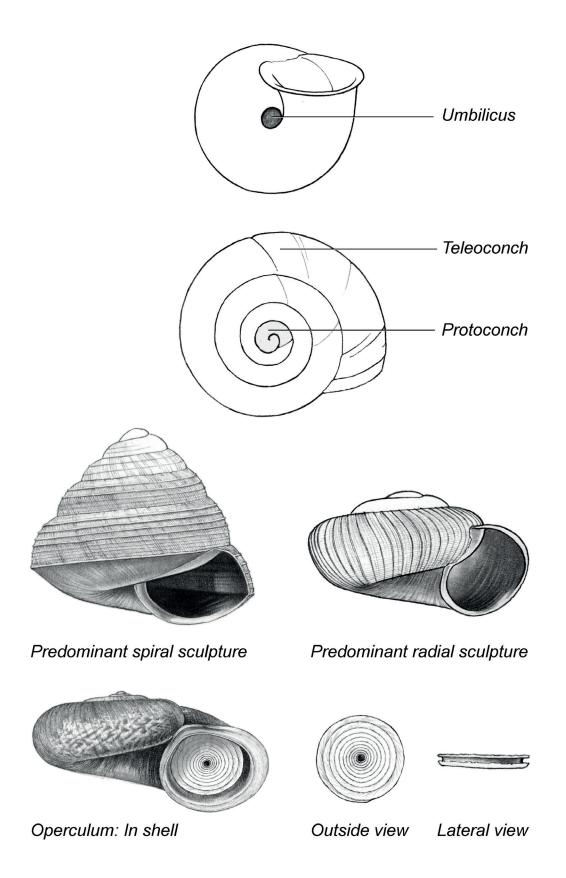


Fig. 4. Terminology.

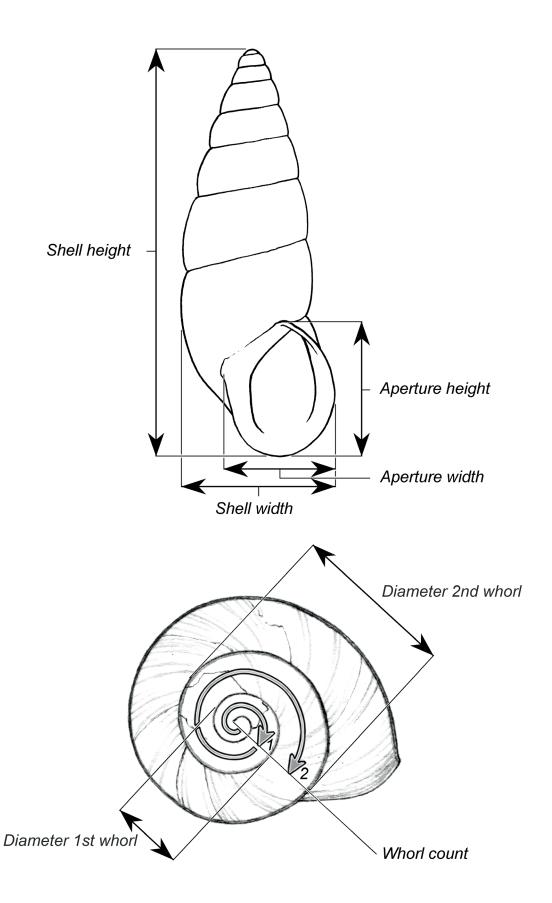
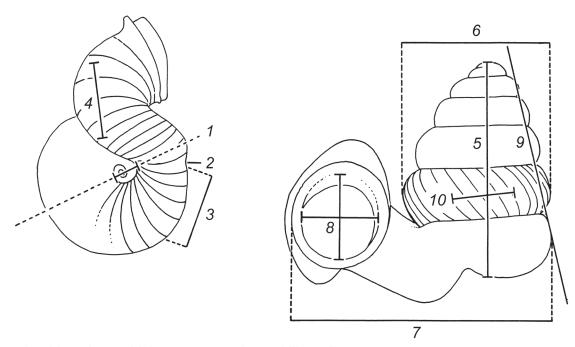
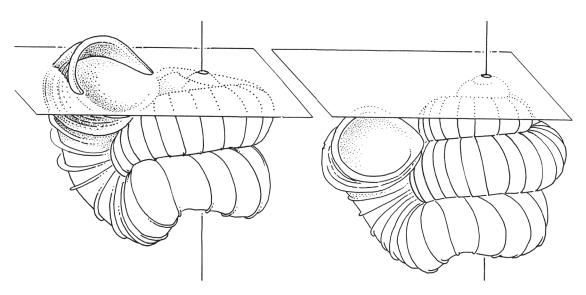


Fig. 5. Measuring shells.



- 1 Line along which to measure the umbilicus diameter
- 2 Constriction
- 3 Number of radial ribs/0.5 mm on the spire, close to the constriction
- 4 Number of radial ribs/0.5 mm half way along the tuba
- 5 Height of spire
- 6 Width of spire
- 7 Width of spire including tuba
- 8 Height and width of aperture
- 9 Line along which convexity of the spire can be assessed
- 10 Number of radial ribs/0.5 mm on the penultimate whorl of the spire



Upper margin peristome above apex of spire Upper margin peristome below apex of spire

Fig. 6. Measuring shells: Diplommatinidae.

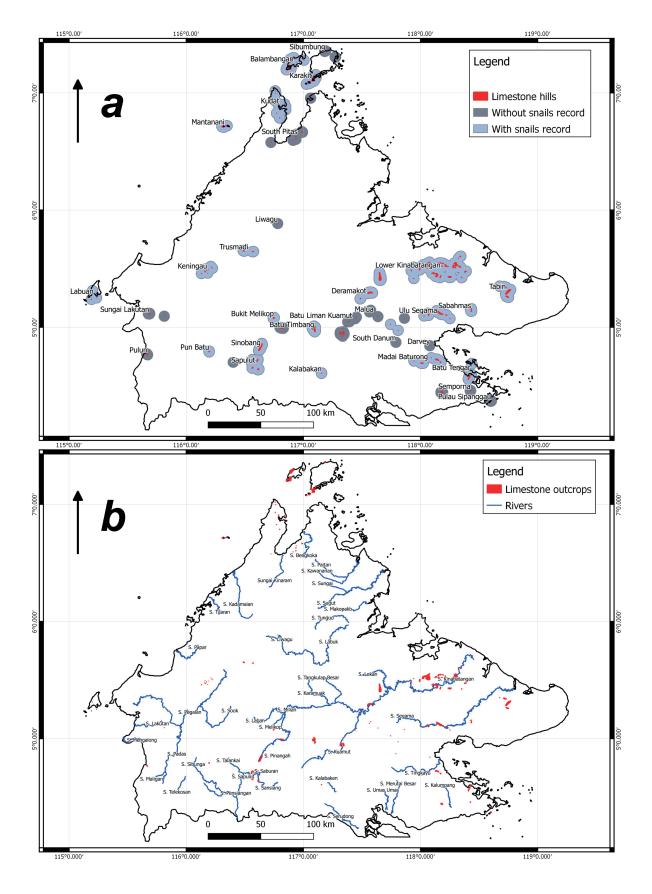


Fig. 7, a. Limestone areas in Sabah. For better visibility the limestone hills (red) have a blue (hill sampled for snails) or grey (hill not sampled for snails) polygon as background; b. Major rivers and limestone hills in Sabah

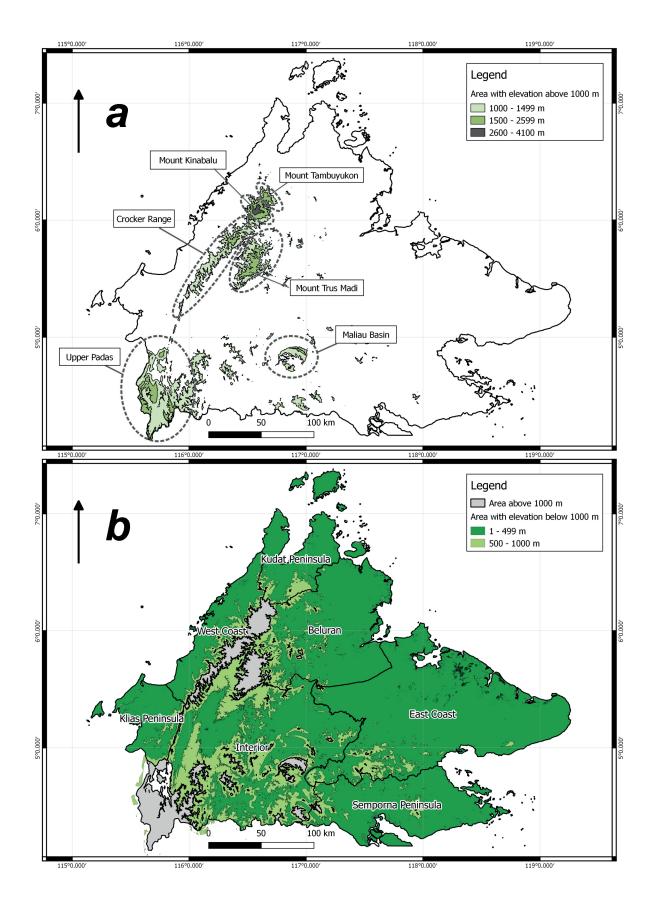


Fig. 8, a. Highlands over 1000 m in Sabah; b. Lowlands below 1000 m in Sabah. Administrative geographical units are also indicated.

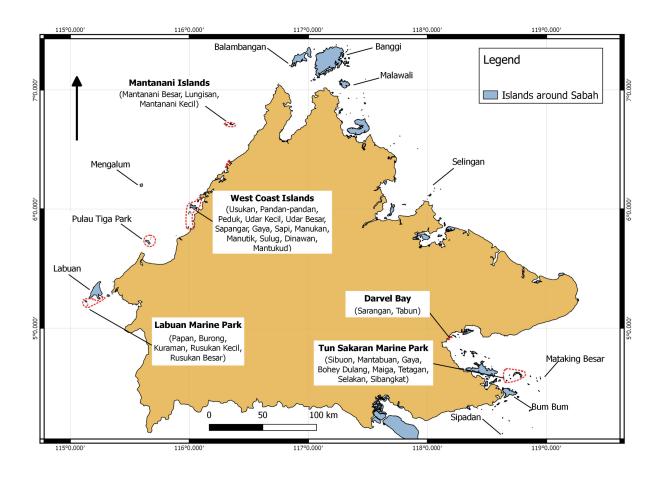


Fig. 9. Islands in Sabah. Six groups are marked with a red dashed line. All islands mentioned on the labels have been sampled for snails.

Identification charts for Sabah land snails

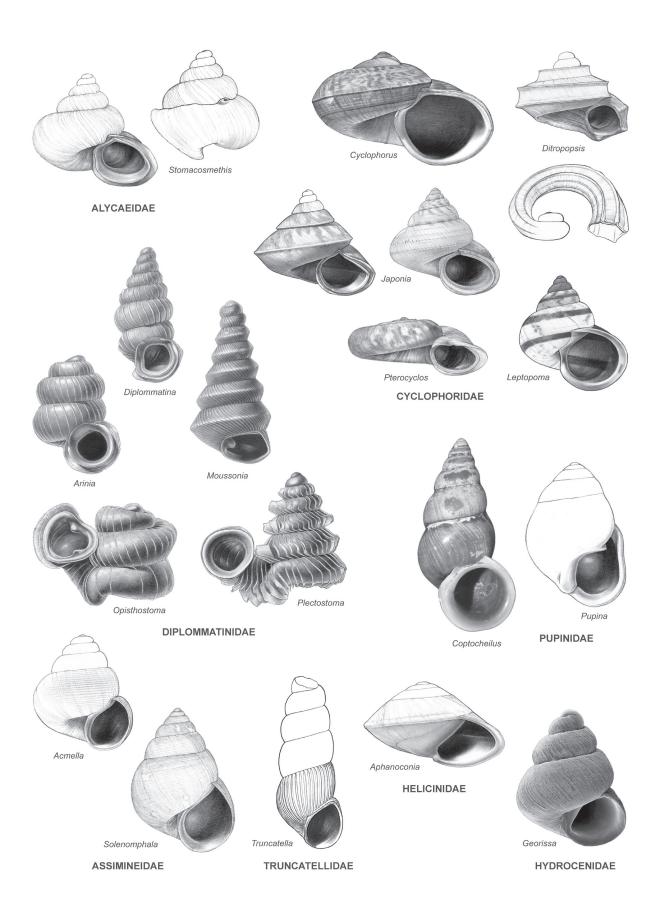


Fig. 10. Identification chart for Sabah land snails: Snails with operculum (Caenogastropoda, Architaenioglossa and Littorinimorpha; Neritimorpha, Cycloneritida).

IDENTIFICATION CHARTS FOR SABAH LAND SNAILS

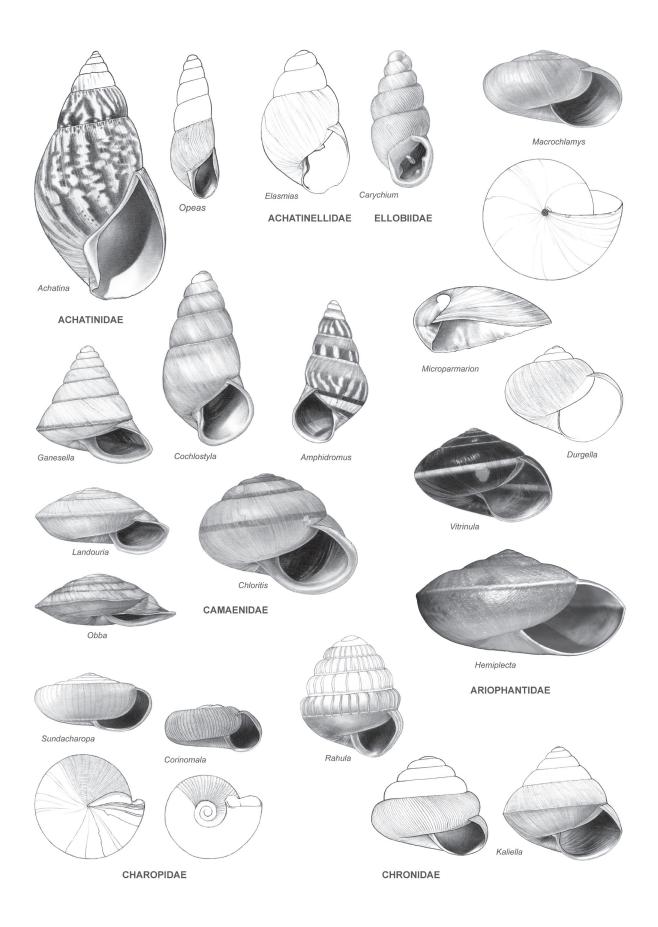


Fig. 11. Identification chart for Sabah land snails: Snails without operculum (Heterobranchia, Ellobiida and Stylommatophora

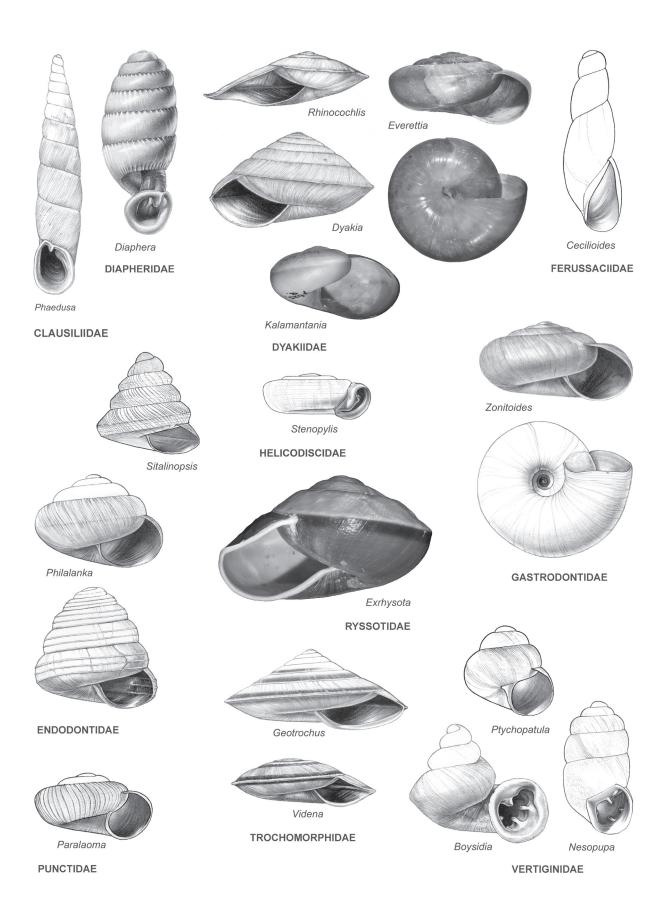


Fig. 12. Identification chart for Sabah land snails: Snails without operculum (Heterobranchia, Stylommatophora).

IDENTIFICATION CHARTS FOR SABAH LAND SNAILS

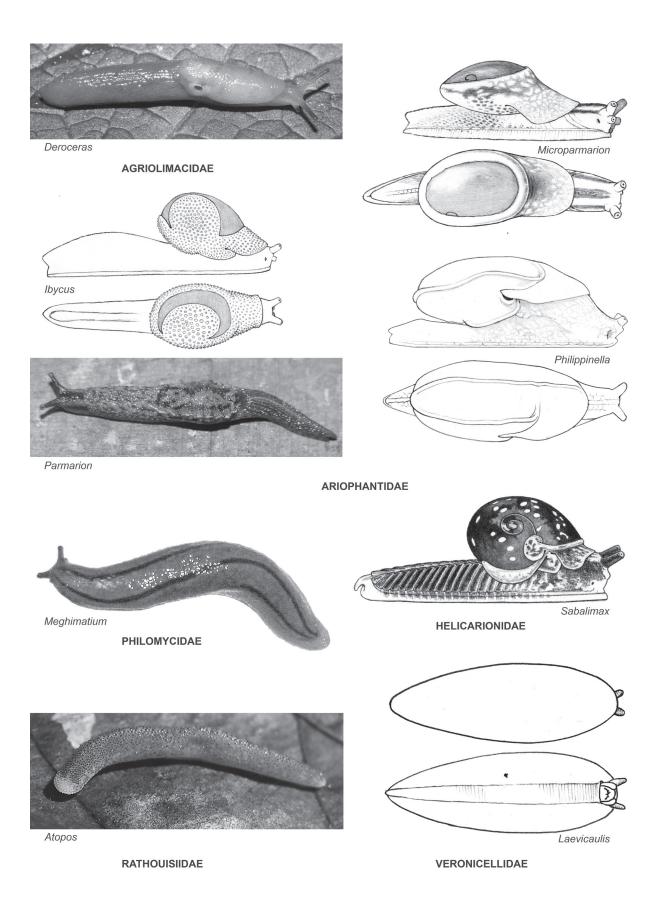


Fig. 13. Identification chart for Sabah land snails: Slugs and semi-slugs (Heterobranchia, Stylommatophora and Systellommatophora).

Keys to the families (Sabah species only)

Notes. 1. Most land snail species are known by their shells only. Therefore, their taxonomy above species level was largely based on shell morphology for a long time, even though it was recognized that the anatomy of the soft parts better reflects phylogenetic relationships. More recently, molecular data have become available for a selection of species. At present, the generally accepted taxonomical framework above species level is a synthesis of these three data types. It is far from complete; the taxonomy of large groups is still based on shell characters only, even though it appears that, of the three data types, shell morphology is the least indicative of phylogenetic relationships.

Shells is all we have of most species, and the keys below primarily use shell characters. Therefore, the keys are sketchy at best, particularly the parts on groups of slugs and semi-slugs.

- 2. Although the key mainly uses shell characters (including characters of the operculum, if present), the key can only be used on material which includes the soft parts because the presence or absence of an operculum needs to be ascertained.
- 3. The key can only be used on adult specimens. Juvenile specimens can usually be recognized by the very thin, fragile palatal peristome, although adults of some thin-shelled species such as *Sabalimax*, *Helicarion* (Helicarionidae) and *Kalamantania* (Dyakiidae) may show the same features. Specimens with a thickened and/or spreading peristome can usually be considered as adults, but check *Diaphera* (Diapheridae), with juvenile specimens developing a thickened peristome, including apertural teeth. In species without a thickened and/or spreading peristome, the peristome of adult individuals is as firm as the shell wall of the last whorl, with a sharp but continuous edge.

1 – Shell entirely absent (slugs)

Key 6

- 1 Shell present (sometimes internal)
 - 2 Animal with operculum

Key 1

- 2 Animal without operculum
 - 3 Animal not fully retractable in its shell. Shell largely or entirely covered by the animal when creeping (Shell often with only few rapidly expanding whorls, or shield-shaped, virtually without whorls) (semi-slugs)

 Key 5
 - 3 Animal fully retractable in its shell. Shell not or only for a small part covered by the animal when creeping (Shell often with 3 or more, slowly expanding whorls) (snails)
 - 4 Aperture with one or more teeth or lamellae

Key 2

- 4 Aperture without teeth or lamellae
 - 5 Either peristome on the palatal side thickened, or peristome spreading, or both characters present **Kev 3**
 - 5 Peristome on the palatal side not thickened, and not spreading

Key 4

Key 1

- 1 Operculum obliquely elliptic, obliquely ovate, or subtriangular, with a clearly excentric nucleus, with few whorls or without whorls
 - 2 Operculum on the inside (i.e. on the side attached to the animal) with a calcareous peg which protrudes beyond the edge of the operculum Family **HYDROCENIDAE**
 - 2 Operculum on the inside without a calcareous peg
 - 3 Shell low conical to lenticular

Family **HELICINIDAE**

- 3 Shell ovoid to (elongated) conical to cylindrical
 - 4 Shell cylindrical with a truncated apex, or shell elongated conical

Family TRUNCATELLIDAE

4 – Shell ovoid to conical

Family ASSIMINEIDAE

- 1 Operculum circular with a central nucleus, with many whorls, or whorls indistinct
 - 5 Spire with a constriction in the last whorl or in the last part of the penultimate whorl, rarely higher up in the spire
 - 6 Constriction with a pore in the inner surface (sometimes not visible without breaking off part of the last whorl), close to the suture, which passes through the shell wall and forms a calcareous tubule in the suture on the outside

 Family ALYCAEIDAE
 - 6 Constriction without a pore in the inner surface

Family **DIPLOMMATINIDAE**

KEYS TO THE FAMILIES

- 5 Spire without a constriction
 - 7 Aperture with a tooth or lamella

Family **PUPINIDAE**

- 7 Aperture without teeth or lamellae
 - 8 Spire elongated-conical with at most moderately convex whorls

Family **PUPINIDAE**

8 – Spire almost flat to somewhat elongated-conical, with convex whorls with or without an angular profile Family CYCLOPHORIDAE

Key 2

- 1 Shell 5.0-27.0 mm high
 - 2 Shell c. 26.5 mm wide

Family CAMAENIDAE (Obba moricandi)

- 2 Shell 1.1–5.1 mm wide
 - 3 Shell greyish brown, dull, 25.5–27.2 mm high
 - 3 Shell white, glossy or shiny, 5.0–8.7 mm high

Family **DIAPHERIDAE**

Family CLAUSILIIDAE

- 1 Shell 0.7-3.0 mm high
 - 4 Shell distinctly wider than high
 - 5 Radial sculpture consisting of growth lines only. Shell white

Family **HELICODISCIDAE**

- 5 Radial sculpture consisting of densely placed, high and narrow ribs. Shell pale to dark brown v Family **CHAROPIDAE** (*Beilania philippinensis*)
- 4 Shell approx. as high as wide, or higher than wide
 - 6 Peristome not thickened and not spreading

Family ACHATINELLIDAE

- 6 Peristome thickened, or peristome spreading, or both characters present
 - 7 Either palatal side of aperture with lamellae well behind the peristome, or shell with a microsculpture of shallow dents

 Family **VERTIGINIDAE**
 - 7 Palatal side of aperture without lamellae behind the peristome. Shell without a microsculpture of shallow dents

 Family ELLOBIIDAE

Key 3

1 - Shell height 1.7-2.3 mm

Family **VERTIGINIDAE** (*Pupisoma lignicola*)

- 1 Shell height 5.5–85 mm
 - 2 Last whorl acutely keeled. Periostracal hair-scars absent (check umbilical area). Aperture forming an angle of 450 or less with the coiling axis
 - 3 Aperture with a distinct spur where the peripheral keel meets the peristome

Family **DYAKIIDAE** (*Rhinocochlis*)

3 – Aperture without a spur where the peripheral keel meets the peristome

Family TROCHOMORPHIDAE

- 2 Either last whorl rounded to angular, or last whorl acutely keeled but then either periostracal hair-scars present (check umbilical area), or aperture forming an angle of 600 or more with the coiling axis
 - 4 Shell width 60–85 mm

Family RYSSOTIDAE

- 4 Shell width 9–33 mm
 - 5 Sculpture above the periphery including fine, rather conspicuous, densely and slightly unevenly spaced, low, rounded radial riblets. Periostracal hair-scars absent (check umbilical area)

Family **DYAKIIDAE** (*Elaphroconcha*)

5 – Either shell without densely placed radial riblets, or sculpture above the periphery including radial riblets, but then periostracal hair-scars present (check umbilical area) Family **CAMAENIDAE**

Key 4

- 1 Shell distinctly higher than wide
 - 2 Shell height 100-170 mm

Family ACHATINIDAE (Achatina)

- 2 Shell height 1.4–20.0 mm
 - 3 Spire conical with straight sides. Spiral sculpture including distinct threads

Family ENDODONTIDAE (Sitalinopsis conulus)

- 3 Spire elongated conical to cylindrical. Spiral sculpture absent, or consisting of fine grooves
 - 4 Either spiral sculpture present, fine, or shell 0.4–0.5 mm wide at 3–4 whorls

Family FERUSSACIIDAE

4 – Spiral sculpture absent. Shell 1.2–2.8 mm wide at 3–4 whorls

KEYS TO THE FAMILIES

- 5 Shell height 6.5–20 mm. Shell usually white to pale corneous Family **ACHATINIDAE**
- 5 Shell height 1.4–2.2 mm. Shell pale (yellowish) brown to brown Family **VERTIGINIDAE**
- 1 Shell approx. as high as wide, or wider than high
 - 6 Last whorl acutely keeled, and shell width 9 mm or more
 - 7 Shell sinistral

Family DYAKIIDAE

- 7 Shell dextral
 - 8 Shell width 9.8–24.4 mm. Sculpture above the periphery an even pattern of radial riblets and/or spiral striation Family **TROCHOMORPHIDAE**
 - 8 Shell width 27–47 mm. Sculpture above the periphery uneven, including small wrinkles and dents Family **ARIOPHANTIDAE** (*Hemiplecta*)
- 6 Either last whorl rounded to obtuse, or last whorl acutely keeled but then shell width 7 mm or less
 - 9 Shell (somewhat depressed) conical to conical-ovoid
 - 10 Either shell with distinct spiral sculpture of 1 or more spiral threads (next to the peripheral keel or thread; finer spiral sculpture may also be present), or umbilicus open, wide and deep, or both characters present

 Family ENDODONTIDAE
 - 10 Shell with fine spiral sculpture (next to a peripheral keel or thread), or without spiral sculpture. Umbilious closed, or umbilious open but very narrow
 - 11 Sculpture inconspicuous or rather distinct, but fine and evenly distributed, often giving the shell surface a silky shine

 Family CHRONIDAE
 - 11 Sculpture rather distinct, giving the shell a rough appearance at 20x magnification

Family **VERTIGINIDAE**

- 9 Shell discoid, (inflated) lenticular to distinctly depressed-conical
 - 12 Shell width 7 mm or less; if shell width 4.2–7.0 mm umbilicus open, (rather) wide
 - 13 Umbilicus open, (rather) wide
 - 14 Radial ribs prominent, high and narrow

Family CHAROPIDAE

- 14 Radial ribs absent, or radial ribs inconspicuous, low and flat
 - 15 Shell 4.2–6.8 mm

Family GASTRODONTIDAE

- 15 Shell width 1.05-2.3 mm
 - 16 Spiral sculpture absent. Radial sculpture virtually absent

Family CHAROPIDAE (Leucocharopion)

- 16 Spiral sculpture present, fine. Radial sculpture with fine riblets the coarsest of which have a periostracal crest Family **PUNCTIDAE**
- 13 Umbilicus closed, or umbilicus open but narrow
 - 17 Radial ribs present, the most prominent with a narrow periostracal crest

Family PUNCTIDAE

- 17 Radial ribs present, all without a periostracal crest, or radial sculpture absent
 - 18 Shell width 1.1–1.9 mm. Last whorl rounded at the periphery. Teleoconch sculpture fine but rather distinct and evenly distributed

Family **CHAROPIDAE** (Sundacharopa)

- 18 Shell width 1.7–3.6 mm; if shell 2 mm wide or less either teleoconch sculpture rather inconspicuous, giving the shell surface an almost smooth appearance, or teleoconch sculpture with predominant, low, fine, unevenly spaced radial riblets, or last whorl angular at the periphery
 - 19 Teleoconch sculpture inconspicuous, giving the shell surface an almost smooth appearance. Last whorl rounded and without peripheral thread

Family ARIOPHANTIDAE (Microcystina)

- 19 Teleoconch sculpture with predominant, low, fine, unevenly spaced radial riblets. Last whorl angular, or with peripheral thread
 - 20 Last whorl angular at the periphery

Family CHRONIDAE (Kaliella phacomorpha)

- 20 Last whorl rounded at the periphery, with or without peripheral thread
 - 21 Radial sculpture consisting of evenly spaced riblets, present on the upper surface of the shell only, rather abruptly fading at the periphery

Family **ARIOPHANTIDAE** (*Microcystina consobrina*)

21 – Radial sculpture consisting of unevenly spaced riblets, present on the upper and lower surface of the shell (but fading close to the umbilicus)

KEYS TO THE FAMILIES

Family ENDODONTIDAE

- 12 Shell width 4.2 mm or more; if shell width 4.2–7.0 mm umbilicus closed, or umbilicus open, very narrow
 - 22 Shell surface above the periphery appearing rough because of uneven, oblique spiral sculpture of fine, wavy, locally braided, shallow, oblique grooves and dents
 - 23 Whorls rapidly expanding, with c. 4 whorls at c. 40 mm shell width

Family **DYAKIIDAE** (*Kalamantania*)

23 – Whorls slowly expanding, with 5 3/8-6 1/4 whorls at 27.5-51.0 mm shell width

Family ARIOPHANTIDAE (Hemiplecta)

- 22 Either shell surface above the periphery appearing smooth, or shell surface with an even sculpture of fine spiral grooves, or shell surface dull with an even radial and/or spiral sculpture
 - 24 Adult shells 4.2–12 mm wide, with 2 1/2–4 1/8 whorls. Whorls usually rather rapidly expanding
 - 25 Spiral sculpture on the last whorl fine but rather distinct, present over most of the last whorl Family **ARIOPHANTIDAE** (*Durgella*)
 - 25 Spiral sculpture on the last whorl inconspicuous except for fine grooves just below the suture Family **HELICARIONIDAE**
 - 24 Either adult shells wider than 12 mm, or adult shells 4.2–12 mm wide and with 4 5/8–5 1/8 whorls. Whorls usually rather slowly expanding
 - 26 Animal when creeping with one or more finger-shaped, mobile appendages on the mantle edge Family **ARIOPHANTIDAE**
 - 26 Animal without finger-shaped appendages on the mantle edge

Family DYAKIIDAE (Everettia)

Key 5 (semi-slugs)

- 1 Tail tip not raised
- 1 Tail tip raised

- 2 –Either shell with c. 3 3/4 whorls and fine but conspicuous sculpture, or shell with up to 1 3/4 whorls

Family ARIOPHANTIDAE

Family AGRIOLIMACIDAE

2 – Shell with 2 1/2–4 1/8 whorl, without spiral sculpture or with only traces of inconspicuous spiral sculpture Family **HELICARIONIDAE**

Key 6 (slugs)

1 – Mantle covering up to approx. half the length of the dorsal side of the animal when creeping

Family **AGRIOLIMACIDAE**

- 1 Mantle covering (almost) the entire dorsal side of the animal when creeping
 - 2 Ventral side undivided: Mantle edges do not reach the substrate when the animal is creeping. Lower tentacles undivided Family **PHILOMYCIDAE**
 - 2 Ventral side divided: Mantle edges (almost) touching the substrate when the animal is creeping. Lower tentacles distally bifid or with a proximal lobe along the lower side
 - 3 Animal not dorsoventrally flattened in section, with dorsal keel

Family RATHOUISIIDAE

3 – Animal dorsoventrally flattened in section, without dorsal keel

Family VERONICELLIDAE

Subclass: CAENOGASTROPODA Order: ARCHITAENIOGLOSSA

Family **ALYCAEIDAE** W T Blanford, 1864

Diagnosis for the Sabah species. Shell dextral, (very) small, (low-)conical; apex obtuse. Constriction present in the last whorl, with a pore in the inner surface, close to the suture, which passes through the shell wall and forms a calcareous tubule lying in the suture on the outside which is closed at the end. Color white to yellow(-orange). Sculpture inconspicuous, or radial sculpture predominant over fine spiral striation. Aperture without teeth. Peristome thickened, spreading. Umbilicus open. Operculum corneous or calcareous, circular, with many whorls; nucleus central.

Notes. 1. See also Cyclostoma spiracellum A Adams & Reeve under Excluded Species.

- 2. See for description and function of the subsutural pore and tubule on the outer shell surface, see Páll-Gergely et al. (2016).
 - 3. We follow the revised generic division of Páll-Gergely et al. (2020).

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Spire on the last whorl with the radial ribs more densely placed near the constriction than elsewhere. Umbilicus wide, 23–38 % of the shell width (measured excluding the spreading peristome) Genus *Chamalycaeus*
- 1 Spire on the last whorl with the radial ribs approx. evenly spaced. Umbilicus narrow, 3–15 % of the shell width (measured excluding the spreading peristome)
 - 2 Radial ribs orthocline

Genus *Pincerna*

2 – Radial ribs prosocline

Genus Stomacosmethis

Genus Chamalycaeus Von Möllendorff, 1897

Diagnosis for the Sabah species. Shell very small, white. Last whorl of spire with the radial ribs more densely placed along the sector where the tubule is attached than elsewhere. Radial ribs (slightly) prosocline. Umbilicus wide, 23–38 % of the shell width without peristome. Shell 1.9–4.0 mm high; number of whorls 3 1/4–4 1/8.

KEY TO THE GROUPS

1 - Shell 2.3-4.0 mm wide

Group 1

1 – Shell 4.2–5.7 mm wide

Group 2

Group 1

Chamalycaeus orthosalpinx Vermeulen & Liew, new species

(fig. 15a-c, map 1a)

Type specimens from Malaysia, Sabah, Interior Prov., Batu Punggol SE of Sapulut (holotype BOR/MOL 292); Malaysia, Sabah, lower Segama river valley, Sabahmas cave (paratypes JV 17647/12 shells).

Chamalycaeus sp. bo-01, Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2761.

Cross diagnosis. Differs from *Chamalycaeus specus* by the almost straight tuba, without a bulge half-way along its upper surface. Also, the last whorl bulges less conspicuously towards the constriction.

Description. Shell very small, somewhat low-conical with concave sides but with the start of the last whorl (slightly) protruding. Whorls evenly rounded, last whorl towards the constriction hardly to moderately bulging below, then slightly narrowed. Constriction inconspicuous, sutural tubule retrorse, 0.4–0.9 mm long. Tuba not or hardly turned downwards, above (almost) without a bulge. Sculpture. Radial sculpture: Growth lines, with rather densely placed to widely spaced (6–16/mm at the periphery on the first part of the last whorl), (rather) distinct, low, thin riblets, but along the sector where the tubule is attached and sometimes some distance beyond the tubule in the direction of the apex with densely placed (3–15/0.5 mm) conspicuous, low riblets; tuba usually with growth lines only, sometimes with up to 8 spaced, low, inconspicuous riblets along the distal part. Spiral sculpture subordinate to the radial sculpture, often most distinct on the last whorl: Moderately and somewhat unevenly spaced, thin threads. Aperture tilted downwards 30–45° relative to the coiling axis of the spire, slightly protruding on the palatal and basal side, slightly to deeply notched where the palatal peristome meets the body whorl. Peristome double, outer peristome widely spreading to somewhat reflexed on the palatal and basal side, inner peristome

slightly to distinctly protruding from the outer, slightly spreading or not. Dimensions. Height 2.0–2.4 mm; width including peristome 2.6–3.3 mm; ratio height/width 0.65–0.79; diameters of the first three whorls 0.50–0.65 mm, 0.85–1.50 mm, 1.8–2.3 mm respectively; umbilicus 0.7–0.9 mm wide, which is 27–32 % of the shell width without peristome; number of whorls 3 1/4–4 including the tuba; height and width aperture 1.1–1.5 mm.

Distribution in Sabah. Rare in S and E: Sapulut, Sabahmas, Tabin. Elevation range: 0–600 m. Disturbed primary forest and secondary woodland on limestone bedrock. Endemic to Sabah.

Name derivation. From ὀρθός (Ancient Greek) = straight, and σάλπιγξ = trumpet.

Chamalycaeus specus (Godwin-Austen, 1889)

(fig. 15d–f, map 1b)

Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Páll-Gergely et al. 2020a: 45; Marzuki et al. 2021: 9. – *Alycaeus specus* Godwin-Austen 1889: 347; Kobelt 1902: 351. – *Alycaeus (Orthalycaeus) specus* (Godwin-Austen) Kobelt & Von Möllendorff 1897a: 148. – Type from Malaysia, Sarawak, 'Jambusan'.

Cross diagnosis. Resembles *Chamalycaeus everetti*, but consistently smaller (shell width including peristome 2.5–4.0 mm, versus 4.5–5.7 mm).

Description. Shell very small, (low-)conical, usually with concave sides because of the (slightly) protruding start of the last whorl. Whorls evenly rounded, last whorl towards the constriction bulging below, then narrowed. Constriction rather inconspicuous, sutural tubule retrorse, 0.6–1.2 mm long. Tuba turned downwards, above with a rather distinct, usually rather narrowly rounded bulge approx. half-way. Sculpture. Radial sculpture: Growth lines, usually with (rather) widely spaced (6-11/mm at the periphery on the first part of the last whorl, more densely placed towards the constriction), usually distinct, low, thin riblets, but along the sector where the tubule is attached and sometimes some distance beyond the tubule in the direction of the apex with densely placed (6-12/0.5 mm)conspicuous, low riblets; tuba with growth lines only, or with up to 12 unevenly spaced, low, inconspicuous to distinct riblets, mainly along the bulging part. Spiral sculpture subordinate to the radial sculpture and sometimes only locally present: Unevenly spaced, thin threads. Aperture tilted downwards approx. 45° relative to the coiling axis of the spire; distinctly protruding on the palatal and basal side, deeply notched where the palatal peristome meets the body whorl. Peristome double, outer peristome widely spreading on the palatal and basal side, inner peristome slightly to moderately protruding from the outer, slightly spreading or not. Dimensions. Height 1.9-3.2 mm; width including peristome 2.5-4.0 mm; ratio height/width 0.65-0.89; diameters of the first three whorls 0.5-0.7 mm, 0.9-1.2 mm, 1.8-2.5 mm respectively; umbilicus 0.6-1.2 mm wide, which is 23-38 % of the shell width without peristome; number of whorls 3 1/2-4 1/8 including the tuba; height aperture 1.0-1.7 mm; width 1.1-1.8 mm.

Distribution in Sabah. Common in E; scattered localities in W but locally common (Sapulut). Elevation range: 0–1200 m. Primary forest, secondary woodland, and degraded vegetation on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Group 2

Chamalycaeus everetti (Godwin-Austen, 1889)

(fig. 14b, 15g-h, map 1c)

Saul 1967: 109; Clements et al. 2008: 2761; Páll-Gergely et al. 2020a: 38. – *Alycaeus everetti* Godwin-Austen 1889: 347; Kobelt 1897: 38. – *Alycaeus (Charax) everetti* (Godwin-Austen) Kobelt & Von Möllendorff 1897a: 150. – *Alycaeus (Dicharax) everetti* (Godwin-Austen) Kobelt 1902: 369; Von Martens 1908: 257. – *Chamalycaeus (Dicharax) everetti* (Godwin-Austen) Zilch 1957: 146. – Type from Malaysia, Sarawak, 'Niah'.

Alycaeus 'n.sp. 7' 'broti' Aldrich 1889: 25. – Chamalycaeus broti (Aldrich) Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41. – Material from Indonesia, Kalimantan.

Chamalycaeus sp. 'V 1599' Schilthuizen 2004: 94; Schilthuizen et al. 2013: Online supplementary data. *Alycaeus* c.f. *rechilaensis* auct. Saul 1967: 109.

[Not Alycaeus rechilaensis Godwin-Austen].

Cross diagnosis. Resembles *Chamalycaeus specus*, but consistently larger (shell width including peristome 4.5–5.7 mm, versus 2.5–4.0 mm).

Description. Shell very small, (somewhat) low-conical with concave sides and with the start of the last whorl slightly protruding; tuba often slightly turned inwards. Whorls evenly rounded, last whorl towards the constriction bulging below, then slightly but rather abruptly narrowed. Constriction distinct, sutural tubule retrorse, (0.8–)1.3–2.0 mm long. Tuba turned downwards, above with a rather distinct, rounded bulge approx. half-way. Sculpture. Radial sculpture: Growth lines, usually with widely spaced (2–6/mm at the periphery on the first part of the last whorl), inconspicuous to distinct, low, thin riblets, but along the sector where the tubule is attached and sometimes

some distance beyond the tubule in the direction of the apex with densely placed (18–30/mm), conspicuous, low riblets; tuba with growth lines only, or with up to 10 widely spaced, inconspicuous to distinct, low riblets along the bulging part. Spiral sculpture subordinate to the radial sculpture and often only locally present: Well-spaced, thin threads. Aperture tilted downwards approx. 45° relative to the coiling axis of the spire; slightly to distinctly protruding on the palatal and basal side, (deeply) notched where the palatal peristome meets the body whorl. Peristome double, outer peristome widely spreading on the palatal and basal side, inner peristome slightly protruding from the outer, slightly spreading or not. Dimensions. Height 3.1–3.9 mm; width including peristome 4.5–5.7 mm; ratio height/width 0.63–0.83; diameters of the first three whorls 0.65–0.90 mm, 1.3–1.7 mm, 2.5–3.7 mm respectively; umbilicus 1.2–1.8 mm wide, which is 27–35 % of the shell width without peristome; number of whorls 3 3/4–4 1/8 including the tuba; height aperture 1.8–2.1 mm; width 1.9–2.7 mm.

Distribution in Sabah. Rather common in E: Lower Kinabatangan and further S; elsewhere Sapulut only but there common. Elevation range: 0–400 m. Also in Sarawak, Kalimantan. Endemic to Borneo.

Chamalycaeus leiodomus Vermeulen & Liew, new species

(fig. 15i-l, map 1d)

Type specimens from Malaysia, Sabah, Sapulut valley, Gua Pungiton (holotype BOR/MOL 287; paratypes JV 7530/6 shells).

Cross diagnosis. Resembles sympatric *Chamalycaeus everetti*; differs by the more elongated-conical spire, and by the not or hardly downwards-turned tuba, with at most a slight bulge half-way along its length. Additionally, the radial sculpture on the spire (except the portion close to the constriction) is much less distinct.

Description. Shell very small, conical with approx. straight or slightly concave sides, with the start of the last whorl often slightly protruding. Whorls evenly rounded, last whorl towards the constriction bulging below, then narrowed. Constriction distinct, sutural tubule retrorse, 0.6–1.0 mm long. Tuba not or hardly turned downwards, above with a slight, rounded bulge approx. half-way along its length. Sculpture. Radial sculpture: Growth lines, in some shells locally with widely spaced (2–3/mm at the periphery on the first part of the last whorl), inconspicuous, low, thin riblets, but along the sector where the tubule is attached with densely placed (9–12/mm) conspicuous, low riblets; tuba with growth lines only. Spiral striation absent, or not visible at 40x magnification. Aperture tilted downwards slightly over 45° relative to the coiling axis of the spire, protruding on the palatal and basal side, notched where the palatal peristome meets the body whorl. Peristome double, outer peristome widely spreading on the palatal and basal side, inner peristome slightly protruding from the outer, slightly spreading or not. Dimensions. Height 3.3–4.0 mm; width including peristome 4.2–4.7 mm; ratio height/width 0.76–0.85; diameters of the first three whorls 0.7–0.8 mm, 1.2–1.5 mm, 2.3–2.8 mm respectively; umbilicus 0.9–1.2 mm wide, which is 24–30 % of the shell width without peristome; number of whorls 3 3/4–4 1/8 including the tuba; height aperture 1.7–2.0 mm; width 1.9–2.2 mm.

Distribution in Sabah. Sapulut only. Elevation range: 300-500 m. In (disturbed) primary forest. Endemic to Sabah.

Name derivation. From λ εῖος (Ancient Greek) = smooth, and δόμος = house, referring to the inconspicuous sculpture on the spire.

Genus *Pincerna* Preston, 1907

Diagnosis for the Sabah species. Shell very small, orange-yellow. Last whorl of spire with the radial ribs approx. evenly spaced. Radial ribs orthocline. Umbilicus narrow, 3–15 % of the shell width without peristome. Shell 4.0–5.0 mm high; number of whorls 3 1/2–4 7/8.

Pincerna globosa (H Adams, 1871)

(fig. 16a-c, map 1e)

Páll-Gergely et al. 2020a: 175; Marzuki et al. 2021: 9. – Alycaeus globosus H Adams 1871 (1870): 794; Issel 1874: 440; Godwin-Austen 1889: 346; Smith 1895: 116 (including varieties kinabaluana, muluana, pygmaea, rabongensis); Kobelt 1902: 345; Saul 1967: 109; Liew et al. 2010: Online Supporting Information, Appendix S1. – Alycaeus (Orthalycaeus) globosus (H Adams) Kobelt & Von Möllendorff 1897a: 147. – Type from Malaysia, Sarawak, 'Busan'.

Alycaeus globosus var. kina-baluana Smith 1895: 116. - Type from Malaysia, Sabah, 'Kina Balu'.

Description. Shell very small, conical with approx. straight sides. Whorls evenly rounded, last whorl towards the constriction bulging below, then gradually narrowed. Constriction distinct, sutural tubule retrorse, 0.4–0.5 mm long. Tuba not turned downwards, gradually widening towards the aperture. Sculpture. Radial sculpture:





Fig. 14, a. Stomacosmethis jagori (E Von Martens, 1860); b. Chamalycaeus everetti (Godwin-Austen, 1889).

Moderately to widely spaced (6–12/mm at the periphery on the first part of the last whorl), distinct, rather low, thin riblets, with the riblets near the constriction approx. similar and similarly distributed but riblets absent on the very last part of the whorl, just before the constriction. Spiral striation not visible at 40x magnification. Aperture tilted downwards up to 15° relative to the coiling axis of the spire, not protruding on the palatal and basal side, not or hardly notched where the palatal peristome meets the body whorl. Peristome double, outer peristome widely spreading on the palatal, basal and columellar side, inner peristome (slightly) protruding from the outer, usually slightly spreading. Dimensions. Height 3.8–5.0 mm; width including peristome 3.6–4.8 mm; ratio height/width 0.98–1.06; diameters of the first three whorls 0.75–0.90 mm, 1.4–1.7 mm, 2.8–3.1 mm respectively; umbilicus 0.1–0.2 mm wide, which is 3–5 % of the shell width without peristome; number of whorls 3 1/2–4 7/8 including the tuba; height aperture 2.1–2.8 mm; width 2.5–2.8 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range; elsewhere in Meliau range only. Elevation range: 300–3000 m. In (disturbed) primary forest on limestone, sand-stone/shale, granodiorite and serpentinite bedrock. Also in Sarawak, Kalimantan (W part). Endemic to Borneo.

Variability. We assume sexual dimorphism in this species, as populations regularly consist of two morphologically distinct forms: A larger with relatively dense radial riblets, and a smaller with more spaced radial riblets. This would be the first case of sexual dimorphism in the family (Páll-Gergely, pers. comm.). Smith (1895:116) named several varieties which partly refer to separate sexes.

Genus Stomacosmethis Bollinger, 1918

Diagnosis for the Sabah species. Shell small, orange-yellow. Last whorl of the spire with the radial ribs approx. evenly spaced. Radial ribs prosocline. Umbilicus narrow, 8–17 % of the shell width without peristome. Shell 4.9–6.8 mm high; number of whorls 4 7/8–5 5/8.

Stomacosmethis jagori (E Von Martens, 1860)

(fig. 14a, 16d–f, map 1f)

Páll-Gergely et al. 2020a: 191. – *Alycaeus jagori* Von Martens 1860 (1859): 208; Pfeiffer 1865: 44; Von Martens 1867: 152; Kobelt 1902: 346; Van Benthem Jutting 1948: 568; Zilch 1957: 147; Maassen 1997: 43; 2001: 22; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – *Alycaeus (Orthalycaeus) jagori* (E Von Martens) Kobelt & Von Möllendorff 1897a: 147. – Type from Indonesia, Java.

Alycaeus (Orthalycaeus) fultoni Von Möllendorff in Smith 1895: 117; Kobelt & Von Möllendorff 1897a: 147; Zilch 1957: 147. – Alycaeus (Alycaeus) fultoni (Von Möllendorff) Kobelt 1902: 343; Solem 1964: 15; Saul 1967: 109. – Stomacosmethis fultoni (Von Möllendorff) Páll-Gergely et al. 2020a: 188. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Alycaeus fultoni var. degenerans Fulton 1901: 242; Kobelt 1902: 539; Zilch 1957: 147; Saul 1967: 109. – Stomacosmethis fultoni degenerans (Fulton) Páll-Gergely et al. 2020a: 189. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

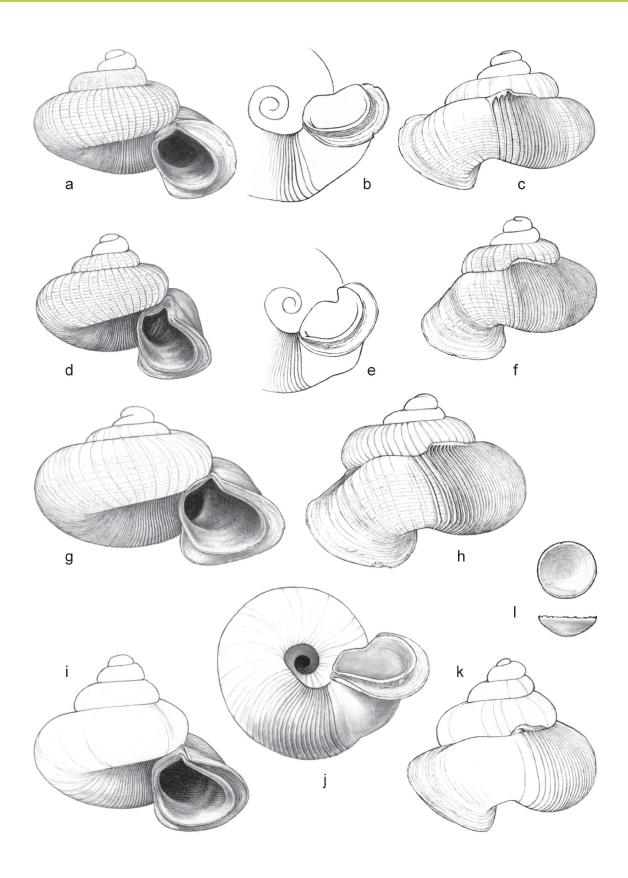


Fig. 15, a–c. *Chamalycaeus orthosalpinx* Vermeulen & Liew, new species, a. Frontal view, shell 2.2 mm high, b. Umbilical view, c. Right lateral view; d–f. *Chamalycaeus specus* (Godwin-Austen, 1889), d. Frontal view, shell 3.0 mm high, e. Umbilical view, f. Right lateral view; g–h. *Chamalycaeus everetti* (Godwin-Austen, 1889), g. Frontal view, shell 3.7 mm high, h. Umbilical view; i–l. *Chamalycaeus leiodomus* Vermeulen & Liew, new species, i. Frontal view, shell 3.6 mm high, j. Umbilical view, k. Right lateral view, l. operculum, above: Outer surface, below: Lateral view.

Description. Shell small, (elongated-)conical with straight or slightly concave sides. Whorls evenly rounded, last whorl towards the constriction bulging below, then distinctly narrowed. Constriction distinct, sutural tubule retrorse, 0.5–0.8 mm long. Tuba not turned downwards, gradually widening towards the aperture, above (almost) without a bulge. Sculpture. Radial sculpture: Growth lines, with (rather) densely placed (8–15/mm at the periphery on the first part of the last whorl), (rather) distinct, low, thin riblets, with the riblets near the constriction approx. similar (although often slightly higher) and similarly distributed; tuba with growth lines only, or with similar but more widely and unevenly spaced riblets on the distal part. Spiral sculpture absent or locally present, subordinate to the radial sculpture, rather densely and somewhat unevenly spaced, thin threads. Aperture tilted downwards 30–45° relative to the coiling axis of the spire, slightly protruding on the upper palatal side, usually slightly notched where the palatal peristome meets the body whorl, sometimes distinctly so. Peristome double, outer peristome somewhat widened to distinctly spreading on the palatal and basal side, inner peristome slightly protruding from the outer, somewhat spreading. Dimensions. Height 4.9–6.8 mm; width including peristome 4.5–7.0 mm; ratio height/width 0.86–1.17; diameters of the first three whorls 0.6–0.8 mm, 1.0–1.3 mm, 1.7–2.2 mm respectively; umbilicus 0.4–0.9 mm wide, which is 8–17 % of the shell width without peristome; number of whorls 4 7/8–5 5/8 including the tuba; height aperture 2.0–3.4 mm; width 2.2–3.7 mm.

Distribution in Sabah. Widespread, scattered localities but locally common (Sapulut, lower Kinabatangan). Elevation range: 0–700 m. Primary and secondary forest, degraded vegetation on limestone and sandstone/shale bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Indonesia (Sumatra, Java, Bali).

Variability. Sabah *Stomacosmethis jagori* is variable, mainly in size and in the height/width ratio. The name *fultoni* refers to relatively large shells, as occur locally in the Kinabatangan river valley. These are otherwise not different from smaller shells referable to *S. jagori*. Intermediates occur.

Notes. Foon et al. (2017) divide material resembling *Stomacosmethis jagori* from Peninsular Malaysia into localized species. In Sabah material we cannot find patterns in character distribution allowing a similar division.

Family **CYCLOPHORIDAE** Gray, 1847

Diagnosis for the Sabah species. Shell dextral, very small to large, conical to discoid with slightly raised apex, apex narrowly obtuse. Constriction in the last whorl absent. Pore in the inner surface, close to the suture and to the aperture, absent or present. Color white to corneous, with or without (red-)brown markings. Sculpture often inconspicuous, or with predominant spiral sculpture over radial sculpture. Aperture without teeth. Peristome often thickened, usually spreading. Umbilicus often open, sometimes closed. Operculum corneous or calcareous, circular, with many whorls; nucleus central.

KEY TO THE GENERA (SABAH SPECIES ONLY)

1 - Shell 1.5-2.8 mm wide

Genus Ditropopsis

- 1 Shell 4-48 mm wide
 - 2 Spire flat, slightly raised, or slightly concave with a raised apex
 - 3 Inner surface of the shell, close to the aperture, with a small pore, which marks the start of a sutural tubule on the outer surface Genus *Opisthoporus*
 - 3 Inner surface of the shell without a pore (even though a sutural tube may be present on the outer surface) Genus *Pterocyclos*
 - 2 Spire low-conical to somewhat elongated-conical
 - 4 Shell 30-48 mm wide

Genus Cyclophorus

- 4 Shell 4–24 mm wide
 - 5 Aperture with a notch in the inner peristome where the palatal peristome meets the body whorl
 - 6 Operculum thick, with a thick calcareous layer on its outer surface

Genus Scabrina

6 – Operculum thin, corneous

Genus Japonia

- 5 Aperture without a notch in the inner peristome where the palatal peristome meets the body whorl
 - 7 Operculum thick, with a thick calcareous layer on its outer surface

Genus Platyrhaphe

7 – Operculum thin, corneous

Genus Leptopoma

Genus Cyclophorus Montfort, 1810

Diagnosis for the Sabah species. Shell (very) large: 30–48 mm wide. Spire (low-) conical. No prominent spiral sculpture. Aperture without a notch in the inner peristome where the palatal peristome meets the body whorl, inside

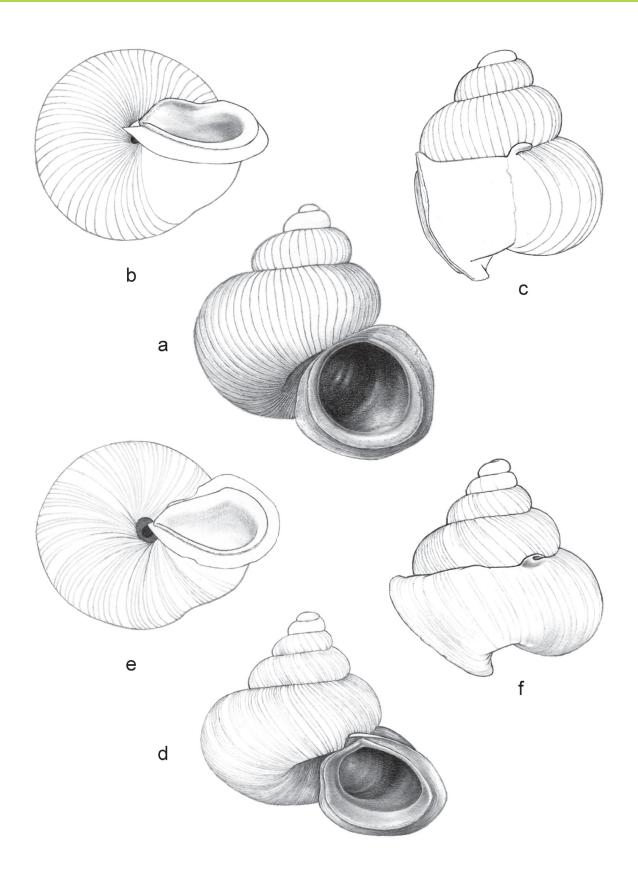


Fig. 16, a–c. *Pincerna globosa* (H Adams, 1871), a. Frontal view, shell 5.0 mm high, b. Umbilical view, c. Right lateral view; d–f. *Stomacosmethis jagori* E Von Martens, 1860, d. Frontal view, shell 6.6 mm high, e Umbilical view, f. Right lateral view.





Fig. 17, a. Cyclophorus kinabaluensis E A Smith, 1895; b. Cyclophorus perdix borneensis (Metcalfe, 1852).

without a pore close to the aperture, outside in the same place without a tubule. Periostracum rather thin, smooth. Operculum thin, corneous.

Cyclophorus kinabaluensis E A Smith, 1895

(fig. 17a, 18a-b, map 2a)

Smith 1895: 118; Schepman 1896: 157; Laidlaw 1937: 186; Vermeulen 1996b: 282; 1999: 144; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Nantarat et al. 2014: 14. – *Cyclophorus (Salpingophorus) kinabaluensis* (Smith) Kobelt & Von Möllendorff 1897b: 109; Kobelt 1902: 129; Von Martens 1908: 256. – Type from Sabah, 'Kina Balu'. *Cyclophorus semisulcatus* auct. Uchida et al. 2013: 52, 53. [Not *Cyclophorus semisulcatus* G B Sowerby I].

Description. Shell large, solid, opaque, white to pale yellow-green to red-brown, often with a narrow brown spiral line around the periphery, and with a few thinner spiral lines above and below the periphery; with or without a faint to very distinct pattern of brown zig-zag lines approx. following the growth lines, this pattern sometimes partly dissolved into a medium brown staining. Surface shiny. Spire low-conical. Whorls rounded, but periphery with a slight to distinct, obtuse to almost sharp edge. Sculpture. Radial sculpture: Growth lines. Spiral sculpture: A fine striation. Aperture: Peristome inconspicuously double, consisting of thin, overlapping lamellae towards the outer peristome, or peristome distinctly double, with the inner peristome protruding up to 2 mm from the outer. Umbilicus open. Dimensions. Height 24–28 mm; width 43–48 mm; umbilicus 7.5–9.0 mm wide; number of whorls 4 1/4–4 3/4; height aperture 18–21 mm; width aperture 21–29 mm. Periostracum pale greenish.

Distribution in Sabah. Widespread, scattered localities. Elevation range: 0–600 m, probably at higher altitude on mount Kinabalu. Primary and secondary forest on limestone and sandstone/shale or granodiorite bedrock. Also in Sarawak, Kalimantan (W part). Endemic to Borneo.

Cyclophorus perdix borneensis (Metcalfe, 1852)

(fig. 17b, 18c–g, map 2b)

Van Benthem Jutting 1959: 69; Saul 1967: 109; Maassen 2001: 11; Vermeulen 1999: 144; Marzuki et al. 2021: 11.

— Cyclostoma borneensis Metcalfe 1852 (1851): 71; Pfeiffer 1854 (1843–1854): 262. — Cyclophorus borneensis (Metcalfe) Pfeiffer 1851d: 139; 1852b: 63; 1852c: 11; 1858: 49; Reeve 1861: Pl. 12, fig. 50; Pfeiffer 1865: 65; Wallace 1865: 413; Von Martens 1867: 136; Issel 1874: 431; Tenison Woods 1888: 1065; Godwin-Austen 1889: 334; Schepman 1896: 157. — Cyclophorus (Glossostylus) borneensis (Metcalfe) Kobelt & Von Möllendorff 1897b: 108. — Cyclophorus (Salpingophorus) borneensis (Metcalfe) Kobelt 1902: 126; Von Martens 1908: 277. — Type from 'Borneo'.

Cyclophorus (Salpingophorus) cochranei Godwin-Austen 1889: 334. – Cyclophorus cochranei (Godwin-Austen) Smith 1895: 119; Von Martens 1908: 256; Nantarat et al. 2014: 7. – Type from Malaysia, Sarawak, 'Busan and Niah Hills'.

Cyclophorus (Salpingophorus) phlegethon Godwin-Austen 1889: 335. – Cyclophorus phlegeton (Godwin-Austen) Von Martens 1908: 256; Nantarat et al. 2014: 19. – Type from Malaysia, Sarawak, Mulu.

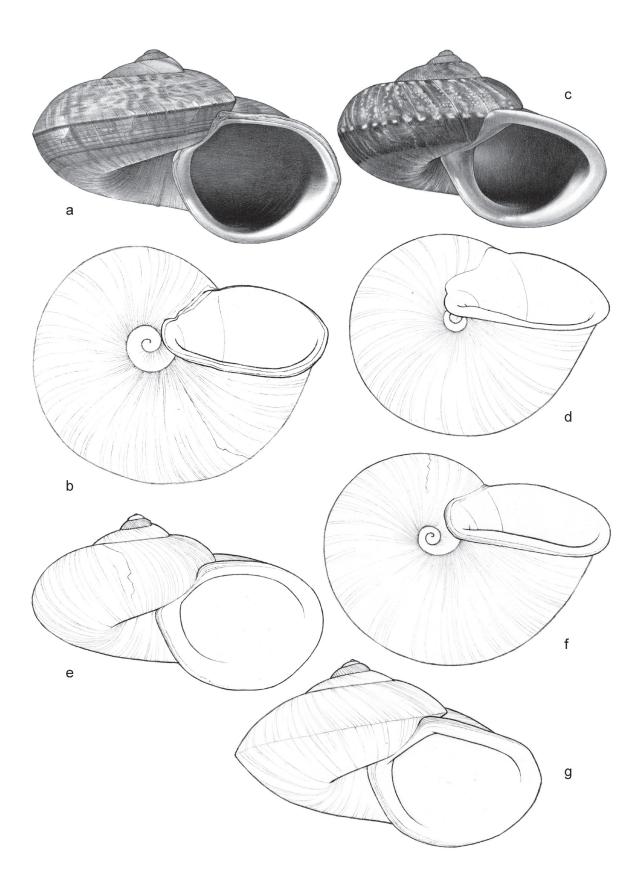


Fig. 18, a–b. *Cyclophorus kinabaluensis* E A Smith, 1895, a. Frontal view, shell 30 mm high, b. Umbilical view; c–g. *Cyclophorus perdix borneensis* (Metcalfe, 1852), c. Frontal view, shell 27 mm high, d. Umbilical view, e. Frontal view, shell 27 mm high, f. Umbilical view, g. Frontal view, shell 32 mm high.

Cross diagnosis. Differs from *Cyclophorus kinabaluensis* by the simple peristome, and by the narrower umbilicus (3.8–7.1 mm wide, versus 7.5–9.0 mm wide).

Description. Shell large, solid, opaque, white to pale yellowish brown, usually with an uneven zig-zag pattern of dark brown, often with a row of pale spots below the suture and at the periphery, with one wide band or two narrower bands of darker brown below the periphery but without continuous, narrow spiral lines. Surface shiny. Spire (low-)conical. Whorls (moderately) rounded, but periphery slightly and obtusely angular to acutely and distinctly keeled. Sculpture. Radial sculpture: Growth lines. Spiral sculpture: A fine striation. Aperture: Peristome simple (because outer and inner peristome fused), without thin lamellae towards the outer margin in fresh shells (sometimes with a few lamellae in the umbilical region). Umbilicus open. Dimensions. Height 19–29 mm; width 30–46 mm; umbilicus 3.8–7.1 mm wide; number of whorls 4 1/2–5; height aperture 14–21 mm; width aperture 16–28 mm. Periostracum very thin.

Distribution in Sabah. Pun Batu only. Old records: Terusan, mount Kinabalu, Labuan. Elevation range: 300–400 m, possibly also in montane conditions. Primary and secondary forest on limestone and sandstone/shale bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Possibly in Malaysia (Peninsula) (Maassen 2001); Singapore; other subspecies in Indonesia (Sumatra, Java, Bali).

Variability. Elsewhere on Borneo, acutely keeled shells occur together with only slightly angular ones. The umbilicus width is also variable.

Note. The most common *Cyclophorus* elsewhere in Borneo, but rare in Sabah.

Genus *Ditropopsis* E A Smith, 1897

(= Ditropis W T Blanford, 1869)

(= Ditropiphorus Fukuda 2000)

Diagnosis for the Sabah species. Shell minute or very small: 1.5–2.8 mm wide. Spire low-conical to somewhat elongated-conical. Spiral keels present. Aperture without a notch in the inner peristome where the palatal peristome meets or is closest to the body whorl; inside without a pore close to the aperture, outside in the same place without a tubule. Periostracum very thin, smooth. Operculum thick, with a calcareous layer.

Note. Ditropis W T Blanford, 1869 is a junior homonym of *Ditropis* Kirschbaum, 1868 (Hemiptera). *Ditropiphorus* Fukuda, 2000 is unacceptable as a replacement name because *Ditropopsis* E A Smith, 1897 has priority.

KEY TO THE GROUPS

1 - Teleoconch whorls entirely detached: Shell an open spiral

Group 1

- 1 Teleoconch whorls (almost) entirely attached
 - 2 Spiral cord above the periphery present

Group 2

2 – Spiral cord above the periphery absent

Group 3

Group 1

Ditropopsis davisoni Vermeulen, Liew & Schilthuizen, 2015

(fig. 19a-b, map 2c)

Vermeulen et al. 2015: 20. - Type from Malaysia, Sabah, upper Padas river valley, Matang river S of Long Pasia.

Cross diagnosis. Uniquely identified among the Sabah snail species by the tubular, detached teleoconch.

Description. Shell very small, rather thick, somewhat translucent, white. Surface shiny. Whorls: Teleoconch whorls entirely detached, approx. in one plane, apex protruding from the plane, distinctly oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 8 keels (description of position of keels as on the first part of the teleoconch, close to the protoconch): 1 supra-peripheral, 1 peripheral, 1 basal, these three distinct, and 5 umbilical, the outer 2 distinct, the inner 3 more inconspicuous; next to these a fine spiral striation on the lower surface. Sculpture continuing up to the peristome. Aperture: Peristome simple (because outer and inner peristome fused), not expanded, angular where the spiral keels meet the peristome. Dimensions. Height c. 0.7 mm; width c. 1.5 mm (both measured along the axis of the teleoconch); height and width aperture c. 0.5 mm.

Distribution in Sabah. Upper Padas only. Elevation range: 1000–1100 m. In montane forest, in a sandstone rock crevice near a small stream in thick leaf litter. Endemic to Sabah.

Group 2

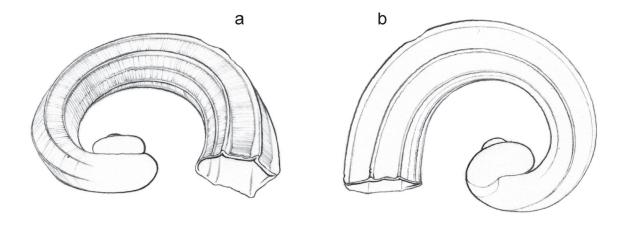


Fig. 19, a-b. Ditropopsis davisoni Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.5 mm wide, b. Back view.

Ditropopsis constricta Vermeulen, Liew & Schilthuizen, 2015

(fig. 20a-b, map 2e)

Vermeulen et al. 2015: 25. – Type from Malaysia, Sabah, Interior Prov., Sapulut valley, Gua Sanaron. *Ditropopsis constricta*, unavailable name, Clements et al. 2008: 2761. *Ditropopsis* sp. 'BO-01', Schilthuizen et al. 2002: 256, 257; Schilthuizen et al. 2003b: 41.

Cross diagnosis. Differs from *Ditropopsis koperbergi* by the constricted aperture, with a distinct radial sculpture. Juvenile shells of *D. constricta*, without a full-grown aperture, have more depressed-conical shells than *D. koperbergi*, with a wider umbilicus.

Description. Shell very small, rather thick, somewhat translucent, off-white to pale greenish yellow. Surface shiny. Spire rather low-conical, apex slightly protruding, slightly oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 4–7 rather inconspicuous to very distinct keels: 1 supra-peripheral and 1 peripheral, about equally wide, 1 basal and 1–4 in the umbilical impression, if fewer than 4 in the umbilical impression then those closest to the basal keel absent; next to these a fine spiral striation on the lower surface. Sculpture continuing up to the peristome, but close to the peristome distorted and partly obliterated by densely placed, low radial riblets in fully adult shells. Aperture: Peristome simple (because outer and inner peristome fused), not expanded, distinctly constricted in fully adult shells, parietal side slightly detached from the penultimate whorl, basal side slightly angular but not drawn-out. Dimensions. Height 1.4–1.6 mm; width 1.8–2.1 mm; ratio height/width 0.78–0.83; umbilicus measured over the basal spiral cord 31–32 % of the shell width; number of whorls 3 7/8–4; height aperture 0.5–0.7 mm; width aperture 0.5–0.75 mm.

Distribution in Sabah. Scattered localities in S: Sapulut, Luasong, Danum valley, Baturong-Madai; elsewhere in Crocker range only. Elevation range: 100–1700 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Also in Brunei, Sarawak, Kalimantan (E part). Endemic to Borneo.

Variability. The drawn specimen has relatively thick spiral keels, specimens with thinner keels occur.

Ditropopsis koperbergi (Zilch, 1955)

(fig. 20c-e, map 2d)

Maassen 2001: 15; Schilthuizen 2004: 94; Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 23; Phung et al. 2017: 62. – *Ditropis koperbergi* Zilch 1955: 193. – Type from Indonesia, Kalimantan, 'Landak'.

Cross diagnosis. Ditropopsis koperbergi is characterized by the absence of densely placed radial riblets close to the peristome.

Description. Shell very small, rather thick, somewhat translucent, white to pale corneous. Surface shiny. Spire conical, apex not protruding, not oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 6–7 rather distinct keels: 1 supra-peripheral and 1 peripheral, about equally wide, 1 basal and 3–4 umbilical; next to these a fine spiral striation on the lower surface. Sculpture continuing up to the peristome. Aperture: Peristome simple (because outer and inner peristome fused),

not expanded, parietal side attached to the penultimate whorl, basal side moderately angular but not drawn-out. Dimensions. Height 1.7–2.1 mm; width 1.9–2.2 mm; ratio height/width 0.85–1.00; umbilicus measured over the basal spiral cord 19–27 % of the shell width; number of whorls 4–4 3/4; height aperture 0.7–0.8 mm; width aperture 0.8–0.9 mm.

Distribution in Sabah. Widespread, rare: Mount Tambuyukon, mount Trus Madi, Danum valley, Tabin. Elevation range: 0–1100 m. In (disturbed) primary forest on limestone and sandstone/shale bedrock. Also in Kalimantan. Endemic to Borneo.

Similar species elsewhere. Among Borneo *Ditropopsis*, the conical spire and the angular whorl profile identify the species.

Note. Maassen (2001) lists a doubtful record from Peninsular Malaysia.

Ditropopsis trachychilus Vermeulen, Liew & Schilthuizen, 2015

(fig. 20f-h, map 2d)

Vermeulen et al. 2015: 22. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., near the km 54 marker on the road Kota Kinabalu-Tambunan, Gunung Mas.

Ditropopsis sp. Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Resembles Ditropopsis koperbergi, but spire more elongated-conical.

Description. Shell very small, rather thick, hardly translucent, pale greenish. Surface shiny. Spire somewhat elongated-conical. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 4 keels: 1 supra-peripheral and 1 peripheral, about equally wide, 1 basal; these all rather distinct; 1 in the umbilical impression, inconspicuous and located deep inside the umbilicus; next to these a fine spiral striation on the lower surface. This sculpture continuing up to c. 0.8 mm from the peristome, to be replaced by densely placed and unevenly spaced radial riblets with a periostracal crest. Aperture: Peristome simple (because outer and inner peristome fused), not expanded, parietal side slightly detached from the penultimate whorl, basal side rounded, hardly drawn-out. Dimensions. Height c. 2.3 mm; width c. 2.0 mm; ratio height/width c. 1.15; umbilicus measured over the basal spiral keel c. 25 % of the shell width; number of whorls c. 4 1/8; height and width aperture c. 0.8 mm.

Distribution in Sabah. Scattered localities in W: Mount Kinabalu, Crocker range, W Coast Islands. Elevation range: 0–3400 m. Coastal woodland, primary montane oak forest on sandstone/shale bedrock; sub-alpine forest on serpentinite and granodiorite bedrock. Endemic to Sabah.

Similar species elsewhere. Ditropopsis gradata Quadras & Von Möllendorff, 1896 and D. pusilla Quadras & Von Möllendorff, 1895, from Philippines, have a similarly high spire and a similar spiral keel distribution. Both species have a more rounded profile to the whorls.

Note. The distinctive sculpture near the aperture develops only when fully adult, as in other species of the genus.

Ditropopsis tyloacron Vermeulen, Liew & Schilthuizen, 2015

(fig. 20i–k, map 2c)

Vermeulen et al. 2015: 23. – Type from Malaysia, Sabah, Tawau Prov., Danum valley Conservation Area. *Ditropopsis* sp. 'BO-02', Schilthuizen et al. 2002: 256, 257.

Cross diagnosis. The low, almost flat spire, with only the apex protruding, characterizes the species among Sabah *Ditropopsis*.

Description. Shell very small, rather thick, somewhat translucent, white to pale (yellowish) green. Surface shiny or glossy. Spire almost flat, but apex protruding, slightly oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 6 very distinct keels: 1 supra-peripheral and 1 peripheral, the latter widest and widely projecting, 1 basal and 3 in the umbilical impression; next to these a fine spiral striation on the lower surface. Sculpture continuing up to the peristome, but towards the peristome distorted and partly obliterated by densely placed, low radial riblets and increasingly coarse spiral threads. Aperture: Peristome simple (because outer and inner peristome fused), not expanded, constricted in fully adult shells, parietal side attached to the penultimate whorl in fully adult shells, basal side angular, slightly to distinctly drawn-out. Dimensions. Height 1.4–1.65 mm; width 2.5–2.8 mm; ratio height/width 0.52–0.56; umbilicus measured over the basal spiral cord 33–37 % of the shell width; number of whorls c. 4; height aperture 0.7–0.9 mm; width aperture 0.8–0.9 mm.

Distribution in Sabah. Danum valley only. Elevation range: 100–200 m. Primary forest on limestone bedrock, rarely on sandstone. Also in Kalimantan (E part). Endemic to Borneo.

Variability. In Kalimantan, the Sabah form (illustrated) locally grades into series with relatively smooth, large shells with the supra-peripheral and umbilical ridges partly or entirely missing. Such shells look a little like Dit-

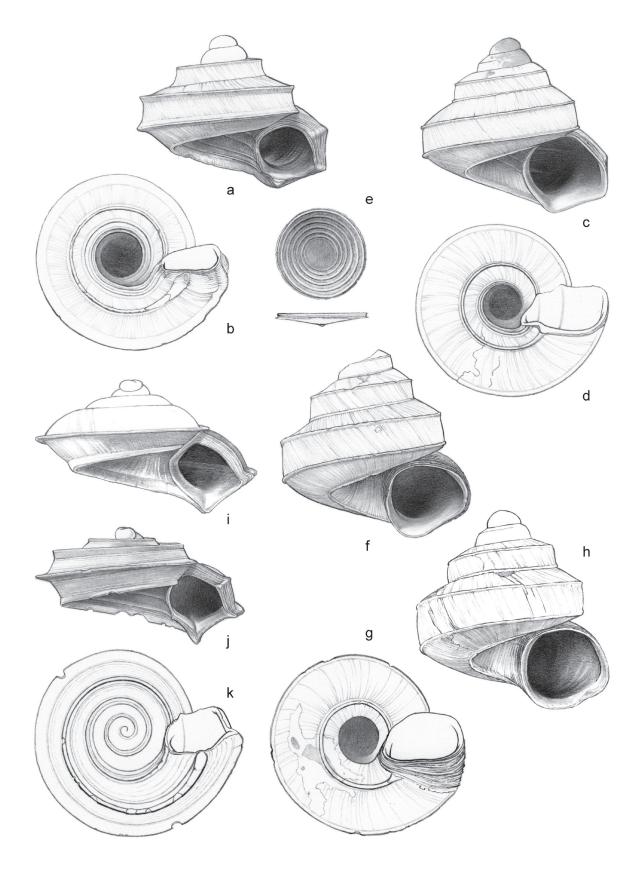


Fig. 20, a—b. *Ditropopsis constricta* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.5 mm high, b. Umbilical view; c—e. *Ditropopsis koperbergi* (Zilch, 1955), c. Frontal view, shell 1.9 mm high, d. Umbilical view, e. Operculum, above: outer surface, below: lateral view; f—h. *Ditropopsis trachychilus* Vermeulen, Liew & Schilthuizen, 2015, f. Frontal view, shell 2.3 mm high, g. Umbilical view, h. Frontal view, shell 2.7 mm high; i–k. *Ditropopsis tyloacron* Vermeulen, Liew & Schilthuizen, 2015, frontal views, i. Shell 1.5 mm high, j. Shell 1.6 mm high, k. Umbilical view.

ropopsis cincta and D. imadatei but have a less elevated spire and a wider umbilicus.

Group 3

Check also:

Ditropopsis tyloacron (Group 2). Specimens without a supra-peripheral cord differ from *D. cincta* and *D. imadatei* by the less elevated spire and wider umbilicus.

Ditropopsis cincta Vermeulen, Liew & Schilthuizen, 2015

(fig. 21a-b, map 2c)

Vermeulen et al. 2015: 26. – Type from Indonesia, Kalimantan Timur, Sangkulirang Peninsula, Liang Belana near Merabu.

Cross diagnosis. The spire height of Ditropopsis cincta is intermediate between D. imadatei and specimens of D. tyloacron without a supra-peripheral cord. Next to this, it differs from D. imadatei by lacking the flaring outer peristome, and from D. tyloacron by its narrower umbilicus.

Description. Shell very small, rather thick, somewhat translucent, corneous to brown. Surface shiny or glossy. Spire low-conical with convex sides, apex protruding, slightly oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 2 very distinct keels: 1 peripheral, widest and widely projecting, 1 basal; next to these fine and inconspicuous spiral striation present, particularly below the suture and around the basal keel. Sculpture continuing up to the peristome, but close to the peristome somewhat distorted because crossed by a few slightly more distinct growth lines. Aperture: Peristome simple (because outer and inner peristome fused), not expanded, parietal side attached to the penultimate whorl, basal side moderately angular and somewhat drawn-out. Dimensions. Height 1.9–2.0 mm; width 2.5–2.7 mm; ratio height/width 0.70–0.76; umbilicus measured over the basal spiral keel 40–48 % of the shell width; number of whorls 4–4 1/2; height aperture 0.8–0.9 mm; width aperture c. 1.0 mm.

Distribution in Sabah. Meliau range only. Elevation range: 100–200 m. Found in primary forest on serpent-inite bedrock. Elsewhere also on limestone bedrock. Also in Kalimantan (E part). Endemic to Borneo.

Ditropopsis imadatei (Habe, 1965)

(fig. 21c–d, map 2f)

Vermeulen et al. 2015: 27; Phung et al. 2017: 63. – *Ditropis imadatei* Habe 1965: 117. – Type from Brunei, Bandar Seri Begawan.

Ditropopsis 'sp. nov.' Schilthuizen 2004: 94.

Cross diagnosis. Uniquely identified among Sabah Ditropopsis by the double peristome.

Description. Shell very small, rather thick, somewhat translucent, white to pale greenish. Surface shiny or glossy. Spire conical with convex sides, apex somewhat protruding, hardly oblique. Sculpture. Radial sculpture: Fine growth lines, locally grading into fine, densely placed riblets. Spiral sculpture on the last whorl: 5(–6) keels: With or without a vaguely marked supra-peripheral, 1 peripheral, 1 basal, very distinct, and 2 much thinner and more inconspicuous keels in the umbilical impression; next to these a fine spiral striation locally present. Sculpture continuing up to the peristome. Aperture: Peristome double, the outer thickened and distinctly expanded, parietal side attached to the penultimate whorl in fully adult shells, basal side angular, distinctly drawn-out; the inner peristome slightly protruding from the outer, slightly expanded, basal side only slightly angular and slightly drawn-out. Dimensions. Height c. 2.0 mm; width 2.0–2.2 mm; ratio height/width c. 0.9; umbilicus measured over the basal spiral keel 25–31 % of the shell width; number of whorls c. 4 1/8; height aperture c. 1.0 mm; width aperture 1.0–1.2 mm.

Distribution in Sabah. Widespread, rare: W Coast Islands, Crocker range, Deramakot F.R. Elevation range: 0–900 m. In primary forest, in coastal woodland, on sandstone/shale and limestone bedrock. Also in Brunei, Sarawak, Kalimantan (E part). Endemic to Borneo.

Similar species elsewhere. Ditropopsis moellendorffi (O Boettger, 1891) (Indonesia, Maluku) has a double peristome, but a much flatter shell with more numerous spiral keels.

Genus Japonia Gould, 1859

Diagnosis for the Sabah species. Shell very small to medium-sized: 4–15 mm wide. Spire (low-) conical. Spiral threads present or absent. Aperture with a notch in the inner peristome where the palatal peristome meets the body whorl, inside without a pore close to the aperture, outside in the same place without a tubule. Periostracum rather thin, smooth or with hairs or scales. Operculum thin, corneous.

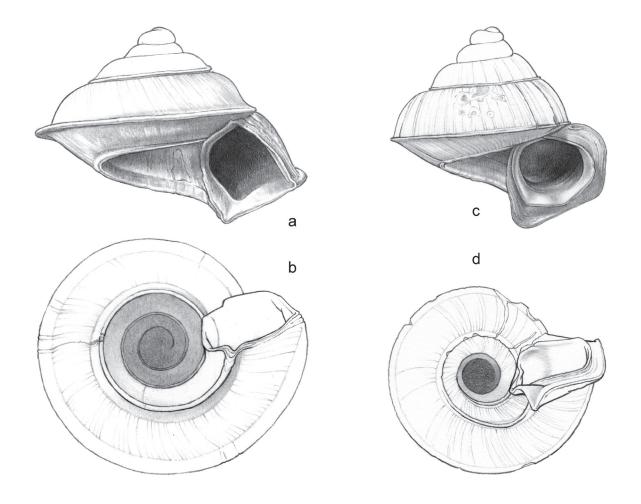


Fig. 21, a–b. *Ditropopsis cincta* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 2.0 mm high, b. Umbilical view; c–d. *Ditropopsis imadatei* (Habe, 1965), c. Frontal view, shell 2.1 mm high, d. Umbilical view.

KEY TO THE GROUPS

- Spiral striation (in between predominant spiral threads) distinct, coarsest in the umbilical impression. Peristome at most only slightly thickened, the outer only slightly spreading
 Group 1
- 1 Either spiral striation absent or fine, or spiral striation distinct but not coarsest in the umbilical impression, and peristome thickened and/or spreading
 - 2 First half of penultimate whorl with 1 predominant spiral thread, close to the suture (next to this a finer spiral striation often present) Group 2
 - 2 First half of penultimate whorl with 2–14 predominant spiral threads, with the lowermost close to the suture (next to these a finer spiral striation often present)
 - 3 First half of penultimate whorl with 2 predominant spiral threads, with the lower close to the suture (next to these a finer spiral striation often present)

 Group 3
 - 3 first half of penultimate whorl with 3–14 predominant spiral threads, with the lower close to the suture (next to these a finer spiral striation often present)
 - 4 Shell 4.0–5.0 mm high. Shell height/width 0.65–0.79

Group 4

4 – Shell 6.3–15 mm high; if shell 7.7 mm high or less, then shell height/width 0.92 or more

Group 5

Group 1

Japonia alticola (Laidlaw, 1937)

(fig. 22a, 23a-b, 30a, map 3a)

Lagochilus alticola Laidlaw 1937: 187; Vermeulen 1996b: 282 ('Lagocheilus'); Tillier & Bouchet 1989 (1988): 256; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, mount Kinabalu, Pakka.

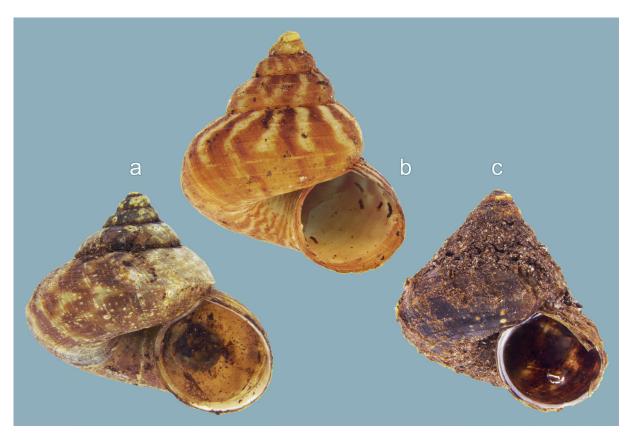


Fig. 22, a. *Japonia alticola* (Laidlaw, 1937), frontal view, shell of animal collected alive; b–c. *Japonia subrudis* Vermeulen & Liew, new species, b. Frontal view, shell after cleaning, c. Frontal view, shell of animal collected alive with soil encrusted on the shell surface.

Description. Shell small, thin, opaque or slightly translucent, white to yellowish, with (dark) red-brown radial blotches, sometimes predominantly (dark) red-brown below the periphery. Surface rather shiny. Spire conical with almost flat to slightly concave sides. Whorls: Apical whorls convex, next whorls moderately convex with the somewhat angular periphery level with the suture or just above it, last whorl at the start angular at the periphery, increasingly rounded towards the aperture, basis narrowly rounded. Whorls not channeled below the suture. Sculpture. Radial sculpture: Distinct, approx. evenly spaced growth lines, some grading into low, rounded radial riblets. Spiral sculpture on the last whorl: 1 distinct, low, knobby peripheral thread, 1-3 similar but less distinct threads above this and 2-5 below, including a basal thread; umbilical impression with up to 5 threads; last whorl from suture to umbilicus also with coarse (only slightly finer than the threads above in some specimens, and particularly coarse in the umbilical impression), densely placed but unevenly spaced, wavy grooves; first half of penultimate whorl with 2-3 threads, the uppermost inconspicuous if three, the lowermost close to the suture. Aperture: Peristome only slightly thickened in fully adult shells, double, the inner at most a thin rim which slightly protrudes from the outer; the outer peristome brown, slightly spreading or not, gradually narrowing in the umbilical region. Dimensions. Height 6.3-7.9 mm; width 7.6-8.8 mm; ratio height/width 0.82-0.90; diameters of the first 3 whorls 0.7-1.0 mm, 1.2-1.7 mm, 2.4-3.2 mm respectively; umbilicus 1.0-1.5 mm wide, 12-17 % of the shell width; number of whorls 4 1/2-5 3/8; height aperture 3.5-4.6 mm; width aperture 3.7-4.6 mm. Periostracum very thin, deciduous, with small, ovate lamellae with a black midvein where radial sculpture crosses the peripheral thread.

Animal. Living animals have smooth shells, not soil-encrusted like Japonia subrudis.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu. Elevation range: 1500–3500 m. In Fagaceae-dominated forest and *Leptospermum* forest on granodiorite bedrock. Endemic to Sabah.

Japonia subrudis Vermeulen & Liew, new species

(fig. 22 b–c, 23c–d, 30b, map 3b)

Type specimens from Malaysia, Sabah, mount Trus Madi, Gua Dawaras (holotype BOR/MOL 1608; paratypes JV 14345/2 shells).

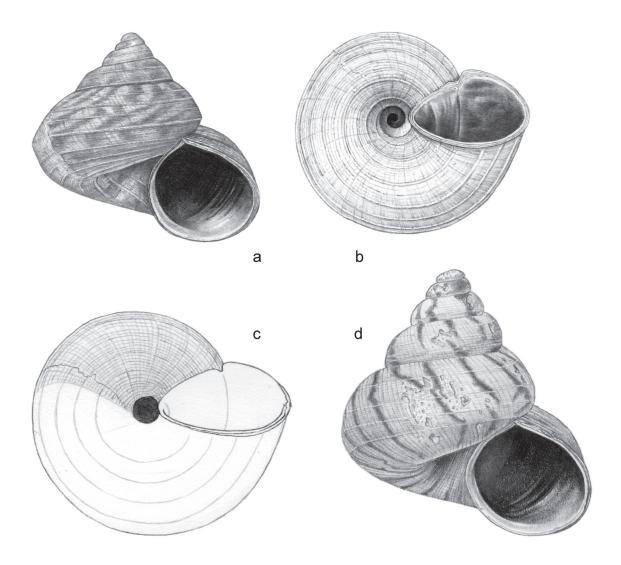


Fig. 23, a-b. *Japonia atticola* (Laidlaw, 1937), a. Frontal view, shell 8.2 mm high, b. Umbilical view; c-d. *Japonia subrudis* Vermeulen & Liew, new species, c. Frontal view, shell 8.5 mm high, d. Umbilical view.

Cross diagnosis. Differs from *Japonia alticola* by the rounded periphery at the start of the last whorl and the more elongated-conical spire (ratio height/width 1.0–1.1, versus 0.82–0.90).

Description. Shell small, thin, opaque, white to pale yellow-green, with pale brown to dark red-brown, narrow to wide radial blotches, sometimes predominantly (pale) brown below the periphery. Surface rather shiny. Spire somewhat elongated-conical with approx. straight to slightly concave sides. Whorls convex with the rounded periphery just above the suture, last whorl half-way rounded at the periphery and at the basis. Whorls not channeled below the suture. Sculpture. Radial sculpture: Distinct, moderately, and approx. evenly spaced growth lines, some grading into low, rounded radial riblets. Spiral sculpture on the last whorl: 6–10 inconspicuous to rather distinct, low threads from the suture to the basis, umbilical impression with up to 3 more such threads close to the basal thread; last whorl from suture to umbilicus also with coarse (only slightly finer than the threads above, and particularly coarse in the umbilical impression), densely placed but unevenly spaced, wavy grooves; first half of penultimate whorl with 3–4 threads, the lowermost (rather) close to the suture. Aperture: Peristome slightly thickened, double, the inner a thin rim which slightly protrudes from the outer; the outer peristome brown, slightly spreading, gradually narrowing in the umbilical region. Dimensions. Height 8.2–9.2 mm; width 8.0–8.4 mm; ratio height/width 1.0–1.1; diameters of the first 3 whorls 0.7–0.9 mm, 1.3–1.6 mm, 2.2–2.6 mm respectively; umbilicus 0.9–1.0 mm wide, 11–13 % of the shell width; number of whorls 5 3/8–6; height aperture 3.5–4.7 mm; width aperture 4.2–4.4 mm. Periostracum very thin, deciduous, no appendages seen in the available material.

Animal. Living animals have shells thickly encrusted with soil.

Distribution in Sabah. Highlands: Mount Kinabalu, Trus Madi range. Elevation range: 1400–3400 m. In mixed primary forest, Leptospermum forest; on limestone and granodiorite bedrock. Endemic to Sabah.

Name derivation. From the prefix sub- (Latin) = a little, and rudis = rough.

Group 2

Check also:

Japonia trilirata (Group 3). Specimens without a spiral thread above the periphery differ from *J. dido* by their smaller size (shell height 4.5–6.5 mm versus 7.4–10.5 mm).

Japonia quinquelirata infracincta (Group 3). Specimens without a spiral thread above the periphery differ from *J. dido* by their smaller size (shell height 6.0–7.0 mm versus 7.4–10.5 mm) and their generally wider umbilicus (14–20 % of the shell width versus 9–13 %).

Japonia anceps Vermeulen, Liew & Schilthuizen, 2015

(fig. 24a-c, map 3a)

Vermeulen et al. 2015: 28. – Type from Malaysia, Sabah, Interior Prov., Crocker Range N.P., Gua Laing c. 12 km N of Keningau.

Japonia 'unidentified' Schilthuizen 2004: 94.

Japonia anceps, unavailable name, Clements et al. 2008: 2761.

Cross diagnosis. Identified within Group 2 by the acutely angular periphery, from the start of the penultimate whorl down to the aperture. *Japonia janus* has an approx. similar shape; it differs by the spiral ridges in the umbilical impression and by the last whorl which is rounded towards the aperture.

Description. Shell small, rather solid, opaque, white to yellowish, with pale brown radial blotches on the upper surface. Surface slightly shiny. Spire conical with concave sides. Whorls: First whorls convex, next whorls almost flat to slightly convex (in large specimens), with the acutely angular periphery just above the suture, last whorl half-way acutely angular at the periphery, slightly convex above and below, basis somewhat obtusely angular. Whorls not channeled below the suture. Sculpture. Radial sculpture: Rather distinct, uneven growth lines, grading into similar radial riblets. Spiral sculpture on the last whorl: 1 distinct, rather thick peripheral thread, 1 somewhat thinner basal thread, immediately above the peripheral thread a slight and inconspicuous spiral striation, immediately below slightly more distinct striation, in the umbilical impression still more distinct striation, grading into densely placed, thin threads; penultimate whorl with 1 distinct peripheral thread, just above the suture. Aperture: Peristome distinctly thickened, double, the inner hardly spreading, a rim which slightly protrudes from the outer; the outer white, moderately spreading, somewhat concave, gradually narrowing in the umbilical region. Dimensions. Height 4.7–6.2 mm; width 5.6–7.1 mm; ratio height/width 0.84–0.88; diameters of the first 3 whorls 0.6–0.7 mm, 1.0–1.2 mm, 2.0–2.4 mm respectively; umbilicus 0.7–1.0 mm wide, 11–13 % of the shell width; number of whorls 4 7/8–5 5/8; height aperture 2.5–2.8 mm; width aperture 2.7–3.5 mm. Periostracum thin, deciduous, no appendages seen in the available material.

Distribution in Sabah. Keningau only. Elevation range: 600–700 m. In secondary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Shares the angular periphery and the whorls which are only slightly convex above and below with *Japonia hyalina* Vermeulen & Junau, 2007, and *J. ditropis* Vermeulen & Junau, 2007, both from Sarawak. It differs from both by its larger size (shell height 4.7–6.2 mm, versus 2.0–3.5 mm), the presence of brown blotches on the shell, as well as by the less conspicuous spiral sculpture apart from the peripheral and basal thread.

Japonia dido (Godwin-Austen, 1889)

(fig. 24d–f, map 3a)

Japonia (Lagochilus) dido (Godwin-Austen) Kobelt 1902: 41; Von Martens 1908: 255. – Lagocheilus dido Godwin-Austen 1889: 338. – Type from Malaysia, Sarawak, 'Niah Hills'

Description. Shell small, rather solid, opaque, white to pale corneous, with or without (red-)brown radial blotches on the upper and lower surface, or lower surface entirely (red-)brown, or entire shell (red-)brown. Surface slightly shiny. Spire conical with approx. straight sides. Whorls convex, last whorl half-way approx. evenly rounded from suture to umbilicus, at the start slightly angular at the periphery in some specimens. Whorls not or hardly channeled below the suture. Sculpture. Radial sculpture: Weak, uneven growth lines, with slightly more prominent ones at uneven intervals. Spiral sculpture on the last whorl: 1 rather inconspicuous to distinct peripheral thread, usually 1 thinner, inconspicuous basal thread, sometimes 1 inconspicuous to rather distinct thread below the peripheral; usually with (traces of) a fine, evenly or unevenly spaced spiral striation; penultimate whorl with 1 distinct peripheral thread, just above the suture. Aperture: Peristome distinctly thickened, double, the inner hardly

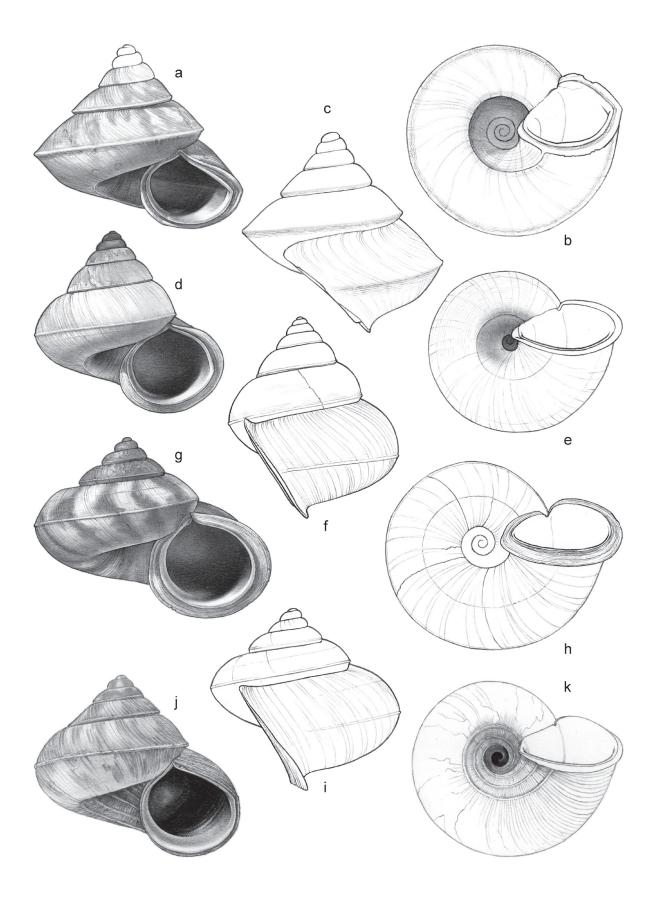


Fig. 24, a–c. *Japonia anceps* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 6.0 mm high, b. Umbilical view, c. Right lateral view; d–f. *Japonia dido* (Godwin-Austen, 1889), d. Frontal view, shell 9.0 mm high, e. Umbilical view, f. Right lateral view; g–i. *Japonia inornata* (E A Smith, 1893), g. Frontal view, shell 6.0 mm high, h. Umbilical view, i. Right lateral view; j–k. *Japonia janus* Vermeulen & Liew, new species, j. Frontal view, shell 7.6 mm high, k. Umbilical view.

spreading, a rim which slightly protrudes from the outer; the outer white, moderately spreading, flat, gradually narrowing in the umbilical region. Dimensions. Height 7.4–10.5 mm; width 7.3–10.5 mm; ratio height/width 0.92–1.06; diameters of the first 3 whorls 0.7–1.0 mm, 1.2–1.6 mm, 2.3–2.8 mm respectively; umbilicus 0.9–1.4 mm wide, 9–13 % of the shell width; number of whorls 5 1/8–5 5/8; height aperture 3.8–5.5 mm; width aperture 3.8–5.8 mm. Periostracum thin, deciduous, with minute hairs where radial riblets cross the peripheral thread.

Distribution in Sabah. Widespread, rare: Meliau range, Sinobang. Elevation range: 100–400 m. In (disturbed) primary forest on limestone and serpentinite bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Sabah material is generally slightly smaller than Sarawak material (shell 7.4–9.0 mm high, versus 8.6–10.5 mm). It is also more vividly colored: Plainly colored shells predominate in Sarawak, shells with brown blotches in Sabah.

Japonia inornata (E A Smith, 1893)

(fig. 22g-i, map 3b)

Japonia (Lagochilus) inornata (Smith) Kobelt 1902: 46; 1907 (1902–1908): 503; Von Martens 1908: 255. – Lagocheilus inornatus Smith 1893b: 345; Kobelt & Von Möllendorff 1897c: 83. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Differs from *Japonia dido* by the wider umbilicus (19–23 % of the shell width, versus 9–13 %). In general, the shell is more depressed-conical.

Description. Shell small, rather thin, opaque, white to pale yellow-corneous, with or without (pale) brown radial blotches on the upper and lower surface. Surface shiny. Spire (somewhat low-)conical with approx. straight to concave sides. Whorls convex with the slightly angular periphery just above the suture, last whorl half-way rounded from suture to umbilicus. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into equally inconspicuous, widely and evenly spaced riblets. Spiral sculpture on the last whorl: 1 fine, distinct, narrow thread at the periphery; above this with or without 1 usually less distinct thread, below the periphery with 2 more threads: One inconspicuous and a more distinct basal thread, umbilical impression without threads; first half of penultimate whorl with 1–2 threads, the lower close to the suture and the upper usually inconspicuous; shell otherwise only locally with traces of inconspicuous, fine, dense spiral striation. Aperture: Peristome thickened, double, the inner a rather thick rim which slightly protrudes from the outer; the outer peristome white to (pale) brown or (pale) red, distinctly spreading, gradually narrowing in the umbilical region. Dimensions. Height 5.5–6.8 mm; width 6.4–8.7 mm; ratio height/width 0.71–0.92; diameters of the first 3 whorls 0.5–0.7 mm, 1.0–1.3 mm, 1.9–2.5 mm respectively; umbilicus 1.2–2.0 mm wide, 19–24 % of the shell width; number of whorls 4 7/8–5 3/8; height aperture 3.0–3.7 mm; width aperture 3.5–4.2 mm. Periostracum thin, deciduous, no appendages seen in most shells, a few very short hairs present on the spiral threads in some.

Distribution in Sabah. Rare in E: Lower Kinabatangan, Lahad Datu, Danum valley. Elevation range: 0–200 m. (Depleted) primary forest and secondary vegetation on limestone bedrock. Endemic to Sabah.

Japonia janus Vermeulen & Liew, new species

(fig. 22j–k, map 3b)

Type specimens from Malaysia, Sabah, Balambangan island (holotype BOR/MOL 3674); ditto, Kok Simpul (paratypes JV 9536/38 shells).

Japonia balabacensis auct. Clements et al. 2008: 2761; Phung et al. 2017: 61; Foon et al. 2018: 95.

Japonia janus, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

Japonia sp. 2 'flat' Schilthuizen et al. 2011: 4. [Not Japonia balabacensis (E A Smith)].

Cross diagnosis. Identified within Group 2 by the presence of 1–5 well-spaced, rather thick spiral threads. Resembles *Japonia anceps*; differs from this species also by the fine spiral striation present on most of the shell surface except the first few whorls.

Description. Shell small, rather thin, opaque, white to pale corneous, with or without (pale) brown radial blotches on the upper and lower surface. Surface slightly shiny. Spire conical with straight or slightly concave sides. Whorls: First whorls convex, next whorls almost flat to slightly convex, with the acutely angular periphery just above the suture, last whorl at the start angular or narrowly rounded at the periphery, increasingly rounded towards the aperture, slightly to moderately convex above the periphery, more distinctly convex towards the aperture, moderately convex below the periphery, basis narrowly rounded. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Rather distinct, uneven growth lines, grading into similar radial riblets. Spiral sculpture on the last whorl: 1 distinct, rather thick peripheral thread, 1 equally thick or somewhat thinner basal thread, 1–5 rather distinct, rather thick threads in the umbilical impression; shell also with a rather distinct,

dense, fine spiral striation; penultimate whorl with 1 distinct peripheral thread, just above the suture. Aperture: Peristome thickened, double, the inner hardly spreading, a rim which slightly protrudes from the outer; the outer white, moderately spreading, gradually narrowing in the umbilical region. Dimensions. Height 6.2–8.0 mm; width 7.0–9.4 mm; ratio height/width 0.85–0.91; diameters of the first 3 whorls 0.65–0.80 mm, 1.1–1.4 mm, 2.0–2.6 mm respectively; umbilicus 1.0–1.7 mm wide, 12–18 % of the shell width; number of whorls 4 7/8–5 1/2; height aperture 3.3–4.3 mm; width aperture 3.5–4.6 mm. Periostracum very thin, deciduous, with small, ovate lamellae with several brown veins where radial sculpture crosses the peripheral thread.

Distribution in Sabah. Balambangan island only. Elevation range: 0–100 m. In dense primary coastal forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Resembles Japonia hyalina Vermeulen & Junau, 2007, and J. ditropis Vermeulen & Junau, 2007, both from Sarawak; see note below J. anceps.

Name derivation. The biconical shape of the shell has inspired the reference to the two-faced Roman god Janus.

Group 3

Check also:

Japonia inornata (Group 2). Shells with a distinct second spiral thread on the first half of the penultimate whorl differ from shells of *J. trilirata kinabaluensis* of less than 7 mm high by the wider umbilicus (19–24 % of the shell width versus 15–18 %), and by the less conspicuous spiral thread above the periphery.

Japonia whiteheadi (Group 5). Shells with only 2 spiral threads on the first half of the penultimate whorl differ from *J. quinqueliratum* by the wider shell (11.5–15 mm wide versus 6.2–8.8 mm) and differ from *J. trilirata kinabaluensis* by the higher shell (10.8–15 mm versus 5.8–9.4 mm) and by the generally narrower umbilicus (11–13 % of the shell width versus 14–21 %).

Japonia monggisensis Vermeulen & Liew, new species

(fig. 25a-c, map 3c)

Type specimen from Malaysia, Sabah, Kinabalu N.P., mount Tambuyukon, near the Monggis-Tambuyukon trail (holotype BOR/MOL 14195).

Cross diagnosis. Characterized within Group 3 by its size (shell height c. 17.7 mm, versus 4–10 mm), by the more rapidly expanding whorls (diameter of the first three whorls c. 1.3 mm, c. 2.1 mm, c. 3.4 mm respectively, versus 0.55–1.0 mm, 1.0–1.5 mm, 1.8–2.6 mm), and by the simple (versus double) peristome. In general appearance and shell size it resembles shells of *Japonia whiteheadi* with only 2 spiral threads on the first half of the penultimate whorl; *J. monggisensis* differs by the same characters as above (diameter of the first three whorls in *J. whiteheadi* 0.7–0.9 mm, 1.4–1. 5 mm, 2.4–2.6 mm), as well as by the absence of a spiral thread on the basal surface of the shell.

Description. Shell medium-sized, thin, somewhat translucent, pale corneous, with a darker apex. Surface shiny. Spire (somewhat elongated-)conical with slightly concave sides. Whorls convex with the rounded periphery just above the suture, basis rounded. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines and very fine, rather densely placed and evenly spaced, low, very narrow riblets. Spiral sculpture on the first part of the last whorl: Traces of 1 fine, narrow thread at the periphery; above this 1 similar thread; first half of penultimate whorl with 2 fine, thin threads, the lower close to the suture; shell also with a fine, rather inconspicuous, dense spiral striation. Aperture: Peristome not thickened, simple (because outer and inner peristome fused), white, spreading, gradually narrowing in the umbilical region. Dimensions. Height c. 17.7 mm; width c. 17.0 mm; ratio height/width 1.00–1.05; diameters of the first 3 whorls c. 1.3 mm, c. 2.1 mm, c. 3.4 mm respectively; umbilicus c. 1.4 mm wide, c. 8 % of the shell width; number of whorls c. 5 3/4; height aperture c. 0.90 mm; width aperture c. 0.97 mm. Periostracum thin, deciduous, locally with short, deciduous hairs on the radial riblets.

Distribution in Sabah. Highlands: Mount Tambuyukon only. Elevation range 1800–1900 m. In primary forest on sandstone/shale bedrock. Endemic to Sabah.

Name derivation. Named after the type locality, the Monggis-Tambuyukon trail.

Japonia quinquelirata quinquelirata (Von Möllendorff, 1887)

(fig. 22d–g, map 3c)

Japonia (Lagochilus) quinquelirata (Von Möllendorff) Kobelt 1902: 52; 1907 (1902–1908): 505. – Lagochilus quinqueliratus Von Möllendorff 1887b: 286; 1894: 213; Smith 1894c: 58; Kobelt & Von Möllendorff 1897c: 84; Zilch 1956: 190. – Type from Philippines, Sulu Archipelago, Bongao.

Lagochilus balabacensis Smith 1895: 121; Kobelt & Von Möllendorff 1897c: 82; Von Möllendorff 1898: 174.

- Japonia (Lagochilus) balabacensis (E A Smith) Kobelt 1902: 35; 1907 (1902–1908): 498. – Type from Philippines, Balabac island.

Lagochilus proprium Fulton 1905: 93. – Japonia (Lagochilus) propria (Fulton) Von Martens 1908: 255. – Type from 'Borneo'.

(?) Lagocheilus conicus auct. Saul 1967: 109.

[Not *Japonia balabacensis* auct. Clements et al. 2008: 2761; Phung et al. 2017: 61; Foon et al. 2018: 95; = *Japonia janus* Vermeulen & Liew].

[Not *Japonia balabacensis* auct. Schilthuizen et al. 2013: Online supplementary data; = *Japonia whiteheadi* (E A Smith)].

[Not Lagochilus conicus E A Smith; nor Cyclotus conicus E Von Martens].

Cross diagnosis. Larger than Japonia trilirata trilirata; like J. trilirata kinabaluensis in size. It differs from the latter by the narrower spire (ratio height/width 1.00–1.17 versus 0.76–0.95), and generally by the narrower umbilicus.

Description. Shell small, rather thin, opaque, white to yellowish brown, usually with (dark) brown radial blotches on the upper and lower surface, the umbilical region sometimes predominantly brown. Surface shiny. Spire somewhat elongated-conical with approx. straight or slightly concave sides, apex not drawn-out. Whorls convex with the rounded periphery just above the suture, last whorl half-way evenly rounded from suture to umbilicus. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Growth lines, grading into unevenly spaced riblets. Spiral sculpture on the last whorl: 1 rather distinct, narrow thread at the periphery; above this 1-3 similar threads, of which 1 approx. as distinct as the peripheral, below the periphery 2-5 more threads, including a distinct basal one; umbilical impression without threads, or with 1-4 threads; first half of penultimate whorl with 2 distinct, thin threads, the lower close to the suture; shell locally also with a fine, dense spiral striation, particularly in the peripheral region and umbilical impression. Aperture: Peristome thickened, double, the inner a rather thin rim which slightly protrudes from the outer; the outer peristome white, spreading, gradually narrowing in the umbilical region. Dimensions. Height (6.5–)8.0–10.0 mm; width (6.2–)7.2–8.8 mm; ratio height/width (1.00–)1.05–1.17; diameters of the first 3 whorls 0.7–1.0 mm, 1.2–1.5 mm, 2.0–2.3 mm respectively; umbilicus 0.5-1.2 mm wide, 8-15 % of the shell width; number of whorls 5-5 5/8; height aperture 3.4-5.2 mm; width aperture 3.8–5.4 mm. Periostracum thin, deciduous, locally with short, thin hairs on the radial riblets, and with small, broadly ovate lamellae without veins where radial sculpture crosses the peripheral thread.

Distribution in Sabah. Rather common in W; elsewhere in Maliau basin only. Elevation range: 0–2300 m. In (disturbed) primary and secondary forest (one record from garden bordering secondary forest) on limestone and sandstone/shale bedrock. Also in Brunei, Sarawak. Endemic to Borneo.

Japonia quinquelirata infracincta Vermeulen & Liew, new subspecies (fig. 22h–k, map 3c)

Type specimens from Malaysia, Sabah, Banggi island, Timbang Dayang (holotype BOR/MOL 13188); ditto, Karakit hill (paratypes JV 1443/16 shells).

Cross diagnosis. Differs from the type subspecies by the slightly drawn-out apex. Also, the shell is usually smaller (5.2-7.5 mm high versus (6.5-)8.0-10.0 mm) and wider (ratio height/width 0.90-1.03 versus (1.00-)1.05-1.17). Differs from the other taxa of Group 3 by the presence of 3-5 distinct threads in the umbilical impression.

Description. Shell small, rather thin, opaque, white to pale yellowish brown, with or without radial blotches of brown above and below, which are most distinct just below the suture. Surface shiny. Spire conical with slightly concave sides, sometimes with almost straight sides, apex slightly drawn-out. Whorls: Apical whorls convex, next whorls moderately convex, somewhat narrowly rounded at the periphery, which is just above the suture, last whorl at the start somewhat narrowly rounded at the periphery, moderately rounded above and below, last half-whorl approx. evenly rounded from suture to umbilicus. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Growth lines, grading into somewhat unevenly spaced, rather distinct riblets. Spiral sculpture on the last whorl: 1 fine, distinct, narrow thread at the periphery; above this 1 similar thread, below the periphery 3 more including the basal thread, one rather close to the basal thread, umbilical impression with 3–5 distinct threads; first half of penultimate whorl with 2 threads, the lower close to the suture, the upper closer to the lower than to the suture above it (observe shell frontally); shell also with a fine, rather dense spiral striation. Aperture: Peristome thickened, double, the inner a rim which slightly to moderately protrudes from the outer; the outer peristome white, somewhat spreading, gradually narrowing in the umbilical region. Dimensions. Height 5.2–7.5 mm; width 5.8–7.3 mm; ratio height/width 0.90-1.03; diameters of the first 3 whorls 0.65-0.70 mm, 1.0-1.3 mm, 1.9-2.1 mm respectively; umbilicus 0.8–1.4 mm wide, 12–18 % of the shell width; number of whorls 4 7/8–5 5/8; height aperture 3.4–3.8 mm; width aperture 3.5–4.0 mm. Periostracum thin, deciduous, with small, semi-elliptic lamellae without

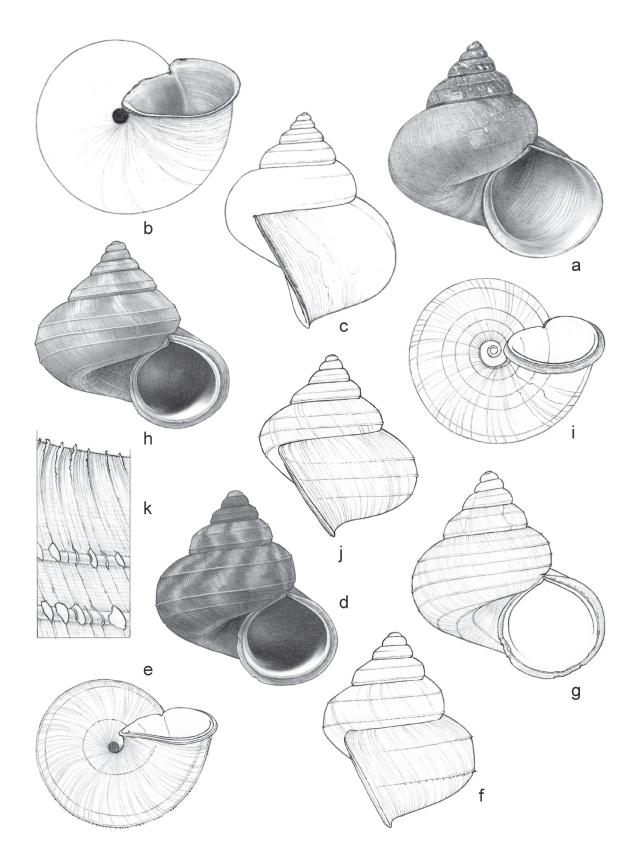


Fig. 25, a–c. *Japonia monggisensis* Vermeulen & Liew, new species, a. Frontal view, shell 17.7 mm high, b. Umbilical view, c. Right lateral view; d–g. *Japonia quinquelirata quinquelirata* (Von Möllendorff, 1887), d. Frontal view, shell 8.0 mm high, e. Umbilical view, f. Right lateral view, g. Frontal view, shell 8.6 mm high; h–k. *Japonia quinquelirata infracincta* Vermeulen & Liew, new subspecies, h. Frontal view, shell 7.0 mm high, i. Umbilical view, j. Right lateral view, k. Sculpture on juvenile shell, part above the periphery.

veins where radial sculpture crosses the threads.

Distribution in Sabah. Banggi island only. Elevation range: 0–100 m. Coastal forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Name derivation. From infra (Latin) = underneath, and cinctus = a belt.

Japonia tambunanensis Vermeulen & Liew, new species

(fig. 26a-b, map 3d)

Type specimens from Malaysia, Sabah, mount Trus Madi, Gua Loloposon (holotype BOR/MOL 14838; paratypes JV 13246/3 shells).

Cross diagnosis. Distinct within Group 3 because of its small size; the largest shells, within the size range of small *Japonia trilirata* have the higher spire (ratio height/width 1.05–1.08, versus 0.76–1.00).

Description. Shell very small, rather thin, opaque, white to corneous, with (dark) brown radial blotches on the upper and lower surface, the umbilical region sometimes predominantly brown. Surface shiny. Spire (somewhat elongated-)conical with approx. straight sides. Whorls convex with the rounded periphery just above the suture, last whorl half-way rounded, basis (somewhat narrowly) rounded. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into similar, widely and evenly spaced riblets. Spiral sculpture on the last whorl: 1 fine, rather distinct, narrow thread at the periphery; above this 1 similar thread, below the periphery 3–4 more including the basal thread, if 4 then the second and third weak or often only present towards the aperture, umbilical impression with or without 1 thread rather close to the basal thread; first half of penultimate whorl with 2 threads, the lower close to the suture; shell also with a fine, dense spiral striation. Aperture: Peristome thickened, double, the inner a rather thin rim which slightly protrudes from the outer; the outer peristome white to brown, spreading, gradually narrowing in the umbilical region. Dimensions. Height 4.0–5.3 mm; width 4.0–4.9 mm; ratio height/width 1.00–1.08; diameters of the first 3 whorls 0.6–0.7 mm, 1.05–1.15 mm, 1.8–2.0 mm respectively; umbilicus 0.3–0.5 mm wide, 9–10 % of the shell width; number of whorls 4 5/8–5 1/8; height aperture 2.2–2.5 mm; width aperture 2.2–2.6 mm. Periostracum thin, deciduous, no appendages seen in the available material.

Distribution in Sabah. Highlands, rare: Crocker range, Trus Madi range. Elevation range: 1100–1600 m. (Disturbed) primary forest on limestone and sandstone/shale bedrock, in damp places. Endemic to Sabah.

Name derivation. Named after Tambunan, a village at the foot of the Trus Madi range.

Japonia trilirata trilirata (L Pfeiffer, 1852)

(fig. 26c–f, 30c, map 3e)

Japonia (Lagochilus) trilirata (L Pfeiffer) Kobelt 1902: 57; Von Martens 1908: 256. – Cyclophorus triliratus Pfeiffer 1852b: 76; Reeve 1861: Pl. 19, fig. 96 – Cyclostoma triliratum (L Pfeiffer) Pfeiffer 1854 (1843–1854): 363. – Cyclotus triliratus (L Pfeiffer) Pfeiffer 1858: 22; Von Martens 1867: 127, 141, 398; Issel 1874: 434; Godwin-Austen 1889: 345. – Lagocheilus triliratus (L Pfeiffer) Nevill 1878: 282; Kobelt & Von Möllendorff 1897c: 82 ('Lagochilus'). – Japonia trilirata (L Pfeiffer) Schilthuizen & Vermeulen 2003a: 95; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data. – Type from Malaysia 'Labuan'.

Cyclostoma quadrifilosum Benson 1852: 270. – Cyclophorus quadrifilosus (Benson) Pfeiffer 1854d: 84. – Japonia trilirata var. quadrifilosa (Benson) Kobelt 1902: 57. – Type from Malaysia, 'Labuan'.

'Japonia trilirata/kinabaluensis species complex' Phung et al. 2017: 60.

Description. Shell small, rather thin, opaque, white to pale yellowish brown to orange-brown, with or without radial blotches of pale orange-brown to dark brown above and below. Surface shiny. Spire conical with approx. straight sides; apex not protruding, or sometimes slightly protruding. Whorls convex with the rounded periphery just above the suture, last whorl half-way approx. evenly rounded from suture to umbilicus. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, grading into evenly spaced, rather inconspicuous riblets. Spiral sculpture on the last whorl: 1 fine, inconspicuous to distinct, narrow thread at the periphery; above this usually 1 similar thread, below the periphery usually 1–3(–5) more, evenly spread, including the basal thread (rarely without threads below the periphery); umbilical impression without threads, or sometimes with 1(–2) threads rather close to the basal thread; first half of penultimate whorl with 2 threads, the lower close to the suture, the upper half-way in between the suture above and the lower, or closer to the suture above, sometimes closer to the lower (observe shell frontally!); shell also with a fine, rather dense spiral striation, often most distinct in the umbilical impression. Aperture: Peristome thickened, double, the inner a rim which slightly to moderately protrudes from the outer; the outer peristome white, distinctly spreading, gradually narrowing in the umbilical region. Dimensions. Height 4.5–7.0 mm; width 4.8–8.0 mm; ratio height/width 0.83–1.00; diameters of the first 3 whorls 0.55–0.80 mm, 1.0–1.5 mm, 2.0–2.6 mm respectively; umbilicus 0.5–1.5 mm wide, 9–20 % of the shell

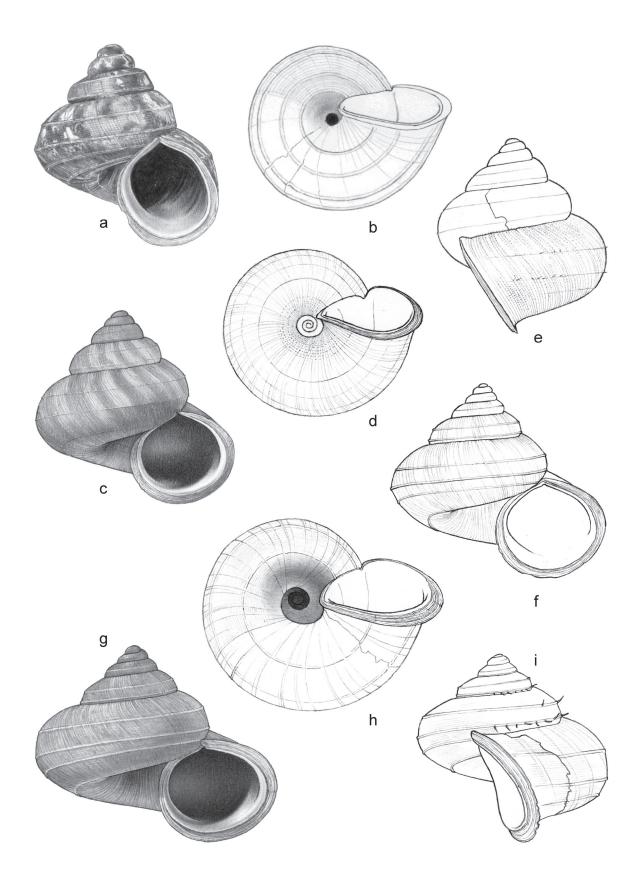


Fig. 26, a–b. *Japonia tambunanensis* Vermeulen & Liew, new species, a. Frontal view, shell 4.2 mm high, b. Umbilical view; c–f. *Japonia trilirata trilirata* (L Pfeiffer, 1852), c. Frontal view, shell 6.5 mm high, d. Umbilical view, e. Right lateral view, f. Frontal view, shell 7.0 mm high; g–i. *Japonia trilirata kinabaluensis* (E A Smith, 1895), g. Frontal view, shell 8.0 mm high, h. Umbilical view, i. Right lateral view.

width; number of whorls 4 3/8–5 3/8; height aperture 2.3–4.0 mm; width aperture 2.5–4.3 mm. Periostracum thin, deciduous, with rather long hairs where radial sculpture crosses the threads.

Distribution in Sabah. Widespread, common. Elevation range: 0–1600 m. In (disturbed) primary forest, secondary forest, coastal forest, also in a fruit garden, on limestone bedrock. Also in Kalimantan. Endemic to Borneo, see below.

Variability. Highly variable in several characters.

- 1. The number of spiral threads in between the peripheral and the basal thread. Some populations consist of shells with two threads (along the lower Segama river and the Tabin river), some consist of shells with more than two threads (lower Kinabatangan river valley), while in others the two morphotypes occur mixed (populations along the W coast, a few along the E coast).
- 2. Scattered populations (e.g., Pun Batu in the Interior Prov., Segarong hills in Tawau Prov.) have a spire with a slightly drawn-out apex, a slightly more narrowly rounded periphery, and the spiral thread above the periphery closer than usual to the peripheral thread. The Pun Batu population also includes shells with 1, sometimes even 2 spiral threads in the umbilical impression. These somewhat resemble *Japonia quinquelirata infracincta* but have fewer threads in the umbilical impression, and they are close to the basal thread, not deep inside the umbilical impression.
- 3. Generally the difference in size between this and subsp. *kinabaluensis*, below, is conspicuous, but a slight overlap exists, see the cross diagnosis with the latter.
 - 4. Some shells lack the uppermost spiral thread but are otherwise not different.

Note. Records from the Aru islands, Indonesia are based on erroneous identifications, see Van Benthem Jutting (1963: 676), under *Lagocheilus tapparonei* C R Boettger, 1922.

Japonia trilirata kinabaluensis (E A Smith, 1895)

(fig. 26g-i, map 3f)

Lagocheilus kina-baluensis Smith 1895: 121; Kobelt & Von Möllendorff 1897c: 83; Vermeulen 1996b: 282 ('Lagochilus'). – Japonia (Lagochilus) kinabaluensis (E A Smith) Kobelt 1902: 46; 1907 (1902–1908) 496; Von Martens 1908: 255. – Japonia kinabaluensis (E A Smith) Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 95. – Type from Malaysia, Sabah, 'Kina Balu'.

Japonia ciliocinctum auct. Schilthuizen 2004: 94.

[Not Cyclophorus ciliocinctus E Von Martens].

Cross diagnosis. Generally larger than Japonia trilirata trilirata, but an overlap in size exists. Small specimens (of approx. 7 mm high) differ from large J. trilirata trilirata by the slightly wider shell (ratio height/width 0.82–0.93 versus 0.97–1.00). Specimens with a rather coarse spiral sculpture may resemble J. quinquelirata infracincta but the number of spiral threads is larger, and they are placed closer together.

Description. As the nominate subspecies, but white to pale corneous to pale orange-brown, often with a darker, purplish apex, a few (in E Sabah) or most (in W Sabah) shells with slightly darker (orange-)brown to dark brown radial blotches on the upper and lower surface, the umbilical region sometimes predominantly brown. Spire conical with approx. straight or slightly concave sides. Sculpture. Spiral sculpture on the last whorl: 1 fine, inconspicuous to distinct, narrow thread at the periphery; above this 1 similar thread, below the periphery 1–2 more including the basal thread, umbilical impression without threads; first half of penultimate whorl with 2 threads, the lower close to the suture the upper usually more closely to the lower than to the suture above (observe shell frontally); shell (locally) also with fine, rather dense spiral striation, often most distinctly present in the umbilical impression. Aperture: Outer peristome white to (red-)brown. Dimensions. Height 6.5–9.4 mm; width 7.5–11.0 mm; ratio height/width 0.76–0.95; diameters of the first 3 whorls 0.60–0.85 mm, 1.1–1.5 mm, 1.8–2.6 mm respectively; umbilicus 1.2–2.2 mm wide, 14–21 % of the shell width; number of whorls 5 1/8–5 7/8; height aperture 3.6–5.0 mm; width aperture 3.8–5.4 mm. Periostracum thin, deciduous, locally with a few short, thin hairs on the radial riblets, and with rather long, thin hairs where radial sculpture crosses spiral threads.

Animal. Living animals have shells thickly encrusted with soil.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–2200 m. In (disturbed) primary forest, coastal woodland, and secondary forest on limestone, volcanic, sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Variability. 1. Shells from Gomantong hill have a fine spiral thread in between the basal thread and the one below the peripheral.

2. Localized populations from the islands N of Semporna lack the spiral thread between the peripheral and the basal thread. Also, the striation in the umbilical impression is coarser than usual in the subspecies.

Similar species elsewhere. Differs from Japonia quinquelirata quinquelirata by the somewhat flattened

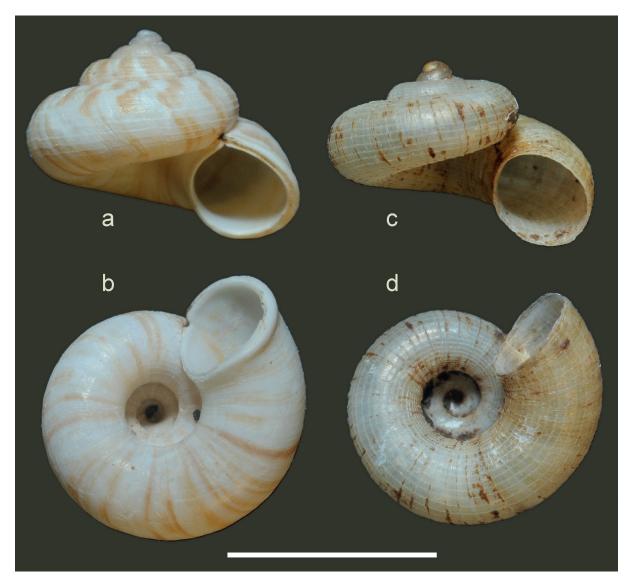


Fig. 27, a-b. *Japonia borneensis* (E A Smith, 1893), a. Frontal view, shell 5.2 mm high, b. Umbilical view; c-d. *Platyrhaphe bongaoensis* (E A Smith, 1894), c. Frontal view, shell 4.5 mm high, d. Umbilical view.

whorls above the periphery.

Note. We include this as a subspecies of *Japonia trilirata* because of the existence of morphologically intermediate shells.

Group 4

Japonia borneensis (E A Smith, 1893)

(fig. 27a-b, 28a-b, map 3d)

Schilthuizen et al. 2011: 4. – *Lagocheilus borneensis* Smith 1893b: 346; Kobelt & Von Möllendorff 1897c: 82 (*'Lagochilus'*). – *Japonia (Lagochilus) borneensis* (E A Smith) Kobelt 1902: 37; 1907 (1902–1908): 506. – Type from Malaysia, Sarawak, 'Barit mountain'.

Lagochilus compressum Von Möllendorff 1894: 213; Kobelt & Von Möllendorff 1897c: 82. – Japonia (Lagochilus) compressa (Von Möllendorff) Kobelt 1902: 39. – Japonia compressa (Von Möllendorff) Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Philippines, Sulu Archipelago, Bongao island.

Japonia keppeli auct. Phung et al. 2017: 61.

[Not Japonia keppeli (Godwin-Austen)].

Cross diagnosis. Specimens without operculum resemble Scabrina serpentinitica, but are smaller, have a more distinct spiral sculpture, and have a shinier shell surface. Juveniles (without a fully developed peristome) may resemble Platyrhaphe bongaoensis, but have distinctly prosocline, not orthocline, radial sculpture. Also, the shells of Platyrhaphe bongaoensis are white, without color pattern. Adults also differ by the detached last part of the last whorl, and by the thin peristome.

Description. Shell small, (rather) thin, opaque, white to pale corneous, with (red-)brown, rather narrow radial blotches above and below. Surface rather shiny. Spire low-conical with approx. straight sides. Whorls convex with the rounded periphery approx. level with the suture, last whorl half-way evenly rounded from suture to umbilicus. Whorls slightly channeled below the suture. Sculpture. Radial sculpture: Growth lines, some grading into distinct, moderately and approx. evenly spaced low radial riblets. Spiral sculpture on the last whorl: 12–16 moderately and approx. evenly spaced, distinct, low, rather thick to thin threads from the suture to the basis, those towards the basis thinner and more widely spaced; in between some of these threads one or a few thinner threads, and traces of a fine striation present; no spiral sculpture in the umbilical impression; first half of penultimate whorl with 7–12 threads, the lowermost close to the suture. Aperture: Peristome moderately to distinctly thickened, double, the inner a thin to thick rim which (slightly) protrudes from the outer; outer peristome white, slightly to distinctly spreading. Dimensions. Height 4.0–5.0 mm; width 5.5–7.7 mm; ratio height/width 0.65–0.79; diameters of the first 3 whorls 0.65–0.70 mm, 1.2–1.4 mm, 2.3–2.8 mm respectively; umbilicus 1.3–2.4 mm wide, 22–31 % of the shell width; number of whorls 4 1/2–4 3/4; height aperture 2.3–3.0 mm; width aperture 2.5–3.4 mm. Periostracum very thin, deciduous, with very short hairs where radial and spiral sculpture cross, most distinctly present in the peripheral region.

Distribution in Sabah. Scattered localities in W: Banggi island, mount Tambuyukon, mount Kinabalu. Elevation range: 0–1200 m. Found in dry coastal forest on limestone bedrock, and in damp mixed primary forest near waterfall, on sandstone/shale bedrock. Also in Sarawak. Distribution elsewhere: Philippines (Sulu Archipelago).

Group 5

Japonia jucunda jucunda (E A Smith, 1893)

(fig. 28c-f, 30d, map 3d)

Japonia jucunda (E A Smith) Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – Lagocheilus jucundus Smith 1893b: 344; Kobelt & Von Möllendorff 1897c: 82; Solem 1964: 1; Saul 1967: 109. – Japonia (Lagochilus) jucunda (E A Smith) Kobelt 1902: 46; 1907 (1902–1908): 504; Von Martens 1908: 2551. – Type from Malaysia, Sabah, 'North Borneo'.

Lagochilus similis Smith 1893a: 352; Godwin-Austen 1893: 33 ('Lagocheilus'); Kobelt & Von Möllendorff 1897c: 84. – Japonia (Lagochilus) similis (E A Smith) Kobelt 1902: 54. – Type from Philippines, Balabac and Palawan.

Lagochilus bangueyensis Smith 1895: 100, 120; Kobelt & Von Möllendorff 1897c: 82. – Japonia (Lagochilus) bangueyensis (E A Smith) Kobelt 1902: 35; Von Martens 1908: 255. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

(?) Cyclophorus c.f. metcalfei auct. Saul 1967: 109.

[Not Cyclophorus metcalfei Issel]

Cross diagnosis. Juveniles may be confused with juvenile *Leptopoma atricapillum*; this may have a similar, though coarser spiral sculpture above the periphery. *Leptopoma atricapillum* also differs by having distinct spiral sculpture below the periphery.

Description. Shell small to medium-sized, rather thin, opaque, white to pale yellowish brown, with (pale) brown radial blotches just below the suture and above the periphery, but in between sometimes absent, often partly smeared to a dark band, just below the periphery sometimes a brown spiral band. Surface shiny. Spire (somewhat low) conical with approx. straight or slightly concave sides. Whorls: Apical whorls convex, next whorls (moderately) convex, somewhat narrowly rounded at the periphery or not, with the periphery just above the suture, last whorl half-way usually somewhat narrowly rounded or slightly and obtusely angular at the periphery, moderately rounded above and below, (somewhat narrowly) rounded at the basis, but sometimes approx. evenly rounded. Whorls shallowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into thin, moderately and evenly spaced, only slightly raised riblets. Spiral sculpture on the last whorl: 1 fine, inconspicuous to distinct, narrow thread at the periphery; above the periphery 3–4 similar well-spaced threads, with or without up to 10 less conspicuous threads in between, below the periphery 1 more thread and

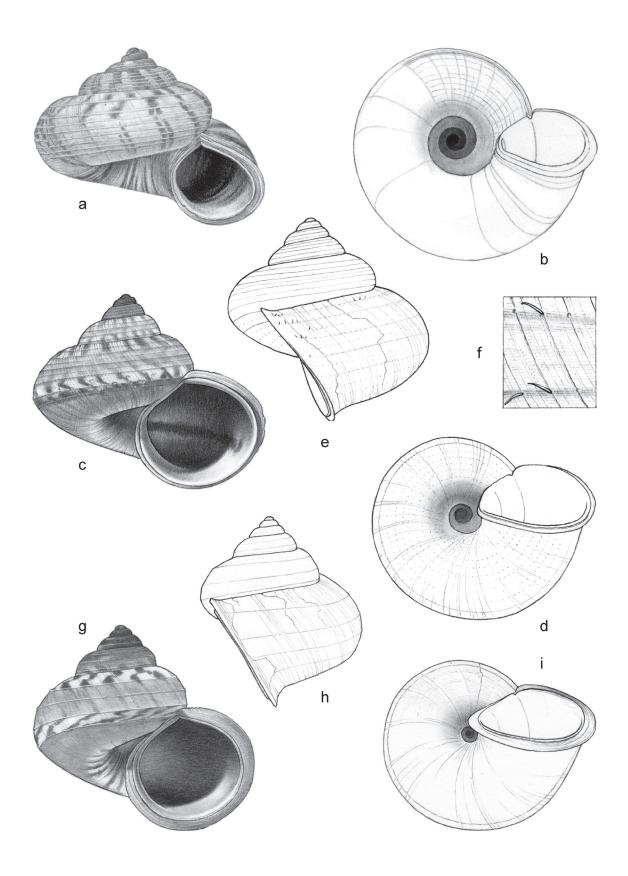


Fig. 28, a–b. *Japonia borneensis* (E A Smith, 1893), a. Frontal view, shell 5.0 mm high, b. Umbilical view; c–f. *Japonia jucunda jucunda* (E A Smith, 1893), c. Frontal view, shell 11 mm high, d. Umbilical view, e. Right lateral view, f. Sculpture on the first part of the last whorl; g–i. *Japonia jucunda meridionalis* Vermeulen & Liew, new subspecies, g. Frontal view, shell 11 mm high, h. Umbilical view, i. Right lateral view.

with or without up to 5 less conspicuous threads, all rather close to the periphery, no spiral threads towards the basis and in the umbilical impression; first half of penultimate whorl with 4–7 threads, the lowermost close to the suture; shell locally also with some very fine striation in between the threads and around the basis. Aperture: Peristome (moderately) thickened, double, the inner a thin to rather thick rim which often slightly protrudes from the outer; the outer peristome white to red(-brown), spreading and gradually narrowing in the umbilical region. Dimensions. Height 7.8–13.2 mm; width 9.7–14.0 mm; ratio height/width 0.75–0.90(–1.02); diameters of the first 3 whorls 0.6–0.9 mm, 1.2–1.7 mm, 2.5–3.2 mm respectively; umbilicus 1.2–2.2 mm wide, 11–18 % of the shell width; number of whorls 4 7/8–5 7/8; height aperture 4.5–7.0 mm; width aperture 5.0–7.3 mm. Periostracum thin, deciduous, with thin hairs where radial riblets cross spiral threads, towards the periphery sometimes with much shorter hairs in between on the radial riblets.

Distribution in Sabah. Rather common in E; elsewhere rare: Balambangan island, Luasong. Elevation range: 0–800 m. (Disturbed) primary forest, shrubby forest, dry coastal forest, and secondary forest, on limestone, sand-stone/shale and volcanic bedrock. Distribution elsewhere: Philippines (Balabac and Palawan islands).

Variability. Variable in size and the ratio height/width. Extralimital shells (Palawan) are up to 19 mm wide.

Japonia jucunda meridionalis Vermeulen & Liew, new subspecies

(fig. 28g-i, map 4a)

Type from Indonesia, Kalimantan Selatan, Meratus mountains, mount Siamang, village Liu c. 30 km E of Tandjung (holotype HNHM 104883, paratypes JV 3085/20 shells).

Cross diagnosis. Narrower than the nominate subspecies (shell width 7.3–8.6 mm, versus 9.7–14.0 mm, and with a narrower umbilicus (0.8–1.0 mm wide, versus 1.2–2.2 mm).

Description. As the nominate subspecies but shell small, with (pale) brown radial blotches just below the suture and below the periphery, but in between sometimes indistinct. Spire conical with straight sides. Whorls: Last whorl at the start approx. evenly rounded. Sculpture. Spiral sculpture on the last whorl: 1 fine, inconspicuous to distinct, narrow thread at the periphery; above the periphery 2–6 similar, moderately to well-spaced threads, below the periphery 2–3 more threads; first half of penultimate whorl with 5–6 threads. Dimensions. Height 7.0–8.0 mm; width 7.3–8.6 mm; ratio height/width 0.92–1.00; diameters of the first 3 whorls 0.75–0.90 mm, 1.4–1.6 mm, 2.6–3.1 mm respectively; umbilicus 0.8–1.0 mm wide, 9–12 % of the shell width; number of whorls 4 5/8–5 1/8; height aperture 4.0–4.5 mm; width aperture 4.3–4.9 mm.

Distribution in Sabah. Sapulut and Sinobang only. Elevation range: 300–500 m. In (disturbed) primary forest, on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. Material from Sabah has evenly rounded whorls, material from elsewhere is somewhat narrowly rounded at the periphery.

Name derivation. From meridionalis (Latin) = southern, referring to the fact that the subspecies occurs further to the South than the type subspecies.

Japonia keppeli (Godwin-Austen, 1889)

(fig. 29a-d, map 4b)

Clements et al. 2008: 2761. – *Lagocheilus keppeli* Godwin-Austen 1889: 338; Kobelt 1897: 30 ('*Lagochilus*'); Kobelt & Von Möllendorff 1897c: 83 ('*Lagochilus*'); Zilch 1955: 188; Saul 1967: 109. – *Japonia (Lagochilus) keppeli* (Godwin-Austen) Kobelt 1902: 46; Von Martens 1908: 255. – Type from Malaysia, Sarawak, 'Niah Hills'.

[Not Japonia keppeli auct. Phung et al. 2017: 61; = Japonia borneensis (E A Smith)].

Cross diagnosis. Smaller than other species of Group 5, compare the shell width of the species. Small specimens of Japonia jucunda meridionalis approach J. keppeli in size but differ by the gradual narrowing of the outer peristome in the umbilical area.

Description. Shell small, rather thin, opaque, white to yellow-corneous, usually without (Sarawak material) or with (Sabah material) (red-)brown radial blotches on the upper and lower surface. Surface shiny. Spire somewhat elongated-conical with approx. straight sides. Whorls convex with the rounded periphery well above the suture, last whorl half-way rounded at the periphery, moderately rounded below, basis rounded. Whorls not channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into similar, well and evenly spaced riblets. Spiral sculpture on the last whorl: 1 fine, inconspicuous to distinct, narrow thread at the periphery; above the periphery 3 similar well-spaced threads, with or without 2 weaker ones in between; below the periphery 7–11 more, the 3–4 closest to the periphery as distinct as the peripheral, with or without a few weaker threads in between, those towards the basis much weaker, including the basal one; first half of penultimate whorl with 5–6 threads, the lowermost close to the suture; shell locally also with some finer striation in between the threads and in the umbilical impression. Aperture: Peristome thickened, double, the inner a thin to thick rim which

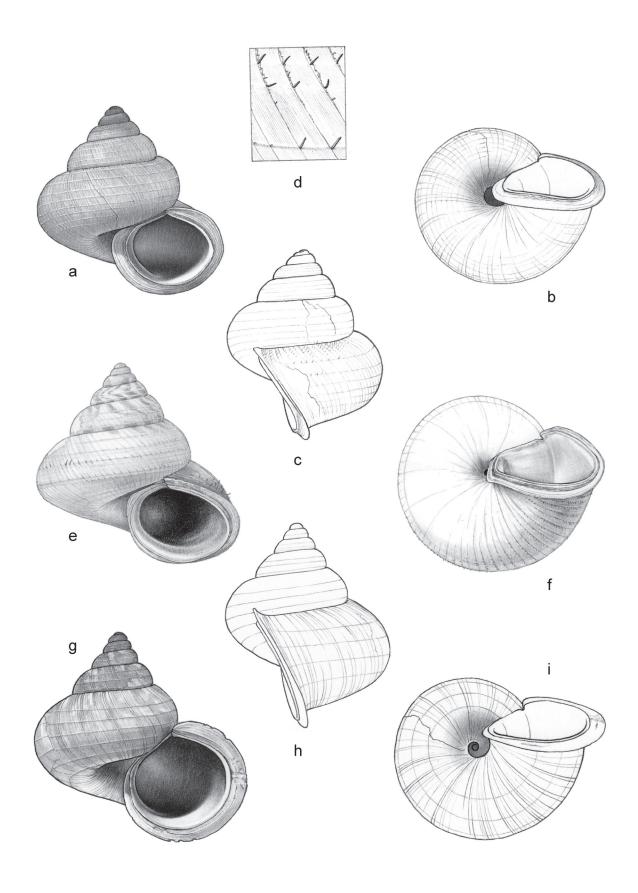


Fig. 29, a–d. *Japonia keppeli* (Godwin-Austen, 1889), a. Frontal view, shell 7.0 mm high, b. Umbilical view, c. Right lateral view, d. Sculpture on the first part of the last whorl; e–f. *Japonia smithi* (Kobelt & Von Möllendorff, 1897), e. Frontal view, shell 10 mm high, f. Umbilical view; g–i. *Japonia whiteheadi* (E A Smith, 1887), g. Frontal view, shell 13 mm high, h. Umbilical view, i. Right lateral view.

often slightly protrudes from the outer; the outer peristome red(-brown), spreading and slightly widened towards the umbilical region before rather abruptly narrowing. Dimensions. Height 6.3–7.8 mm; width 5.8–7.2 mm; ratio height/width 1.00–1.10; diameters of the first 3 whorls 0.65–0.70 mm, 1.0–1.2 mm, 1.7–2.0 mm respectively; umbilicus 0.3–0.9 mm wide, 5–13 % of the shell width; number of whorls 5 3/8–5 7/8; height aperture 2.7–3.8 mm; width aperture 3.3–3.9 mm. Periostracum thin, rather deciduous, with rather long, straight, thin hairs where radial riblets cross spiral threads, and with much shorter hairs in between on the radial riblets.

Distribution in Sabah. Common in Sapulut and Sinobang; rare elsewhere: Meliau range, Tawau hills. Elevation range: 0–600 m. Primary and secondary forest on limestone, sandstone/shale and serpentinite bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Sabah shells have a wider umbilicus than Sarawak shells (0.6–0.9 mm, or 9–13 % of the shell width, versus 0.3–0.4 mm, or 5–7 %), and a more vivid coloration.

Note. In Sarawak known only from Gunung Subis N.P. (illustrated shell).

Japonia smithi (Kobelt & Von Möllendorff, 1897)

(fig. 29e–f, map 4c)

Clements et al. 2008: 2761. – Lagochilus conicus Smith 1895: 121; Vermeulen 1996b: 282 ('Lagocheilus'). – Lagochilus smithi Kobelt & Von Möllendorff 1897c: 84. – Japonia (Lagochilus) smithi (Kobelt & Von Möllendorff) Kobelt 1902: 54; 1907 (1902–1908): 497; Von Martens 1908: 256. – Japonia conica (E A Smith) Schilthuizen & Vermeulen 2003a: 95; Schilthuizen 2004: 94. – Type from Malaysia, Sabah, 'Kina Balu'.

[Not Cyclotus conicus E Von Martens].

[Not Lagocheilus conicus auct. Saul 1967: 109; =? Japonia quinquelirata quinquelirata (Von Möllendorff)].

Cross diagnosis. Shares with Japonia keppeli the rather abruptly narrowing of the outer peristome towards the umbilical region but has a wider shell (7.8–10.0 mm wide versus 5.8–7.2 mm). Japonia jucunda generally has a wider umbilicus; subsp. meridionalis approaches J. smithi in this character but differs in the gradually narrowing outer peristome towards the umbilical region.

Description. Shell small, rather thin, opaque, white to yellow-corneous, with or without pale brown, narrow radial blotches above the periphery. Surface shiny. Spire somewhat elongated-conical with approx. straight sides. Whorls convex with the rounded periphery just above the suture, last whorl half-way (somewhat narrowly) rounded at the periphery, slightly to moderately rounded below, basis rounded. Whorls narrowly channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into similar, well and often evenly spaced riblets. Spiral sculpture on the last whorl: 1 very fine, inconspicuous thread at the periphery, often interrupted by small pits at regular intervals, or consisting only of a row of minute pits; above the periphery (traces of) 2–3 more similar threads, below the periphery 5–8 more, the most conspicuous close to the periphery; first half of penultimate whorl with 3-5 threads, the lowermost close to the suture; shell locally also with a very fine, inconspicuous, shallow spiral striation, particularly above the periphery. Aperture: Peristome thickened, double, the inner a thin rim which often slightly protrudes from the outer; the outer peristome red(-brown), somewhat spreading and with a rounded lobe towards the umbilical region before rather abruptly narrowing. Dimensions. Height 7.7–10.5 mm; width 7.8-10.0 mm; ratio height/width 0.92-1.11; diameters of the first 3 whorls 0.6-0.8 mm, 1.0-1.3 mm, 1.7–2.1 mm respectively; umbilicus 0.4–0.8 mm wide, 4–8 % of the shell width; number of whorls 5 7/8–6 5/8; height aperture 3.5-4.8 mm; width aperture 4.2-5.5 mm. Periostracum thin, rather deciduous, with short, thin hairs where radial riblets cross spiral threads, and with shorter hairs in between.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–400 m. Primary and secondary forest on limestone, sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Japonia whiteheadi (E A Smith, 1887)

(fig. 29g–i, map 4a)

Leptopoma whiteheadi Smith 1887a: 133; 1887b: 221; Godwin-Austen 1889: 337; Kobelt 1902: 33; 1902 (1902–1908): 448; Laidlaw 1937: 186; Vermeulen 1996b: 284; 1999: 157. — Leptopoma (Trocholeptopoma) whiteheadi (Smith) Kobelt & Von Möllendorff 1897c: 82; Kobelt 1902: 33; Von Martens 1908: 255. — Type from Malaysia, 'northern Borneo', presumably Sabah. The collector, Whitehead, did not venture into the then Dutch E Indies according to Van Steenis-Kruseman & Van Steenis (1950: 571).

Japonia balabacensis auct. Schilthuizen et al. 2013: Online supplementary data.

Japonia sp. 1 Schilthuizen et al. 2011: 4.

[Not Japonia balabacensis (E A smith)].

Cross diagnosis. Characterized within Group 5 by the presence of a thin basal thread. Large *Japonia jucunda jucunda* also differ by the larger number of spiral threads above the periphery (3–4 and often a few less conspicuous threads, versus 1–2).



Fig. 30, a. *Japonia alticola* (Laidlaw, 1937); b. *Japonia subrudis* Vermeulen & Liew, new species, juvenile; c. *Japonia trilirata trilirata* (L Pfeiffer, 1852); d. *Japonia jucunda jucunda* (E A Smith, 1893); e. *Leptopoma undatum* (Metcalfe, 1852); f. *Leptopoma undatum* (Metcalfe, 1852), juvenile; g. *Leptopoma atricapillum* (G B Sowerby I, 1843); h. *Leptopoma perlucidum* (Grateloup, 1840).

Description. Shell medium-sized, rather thin, opaque, white to pale yellowish brown, with a darker, or dull purple apex; with (pale) brown radial blotches above and below, or just below the suture and brown lower down. Surface shiny. Spire somewhat elongated-conical with slightly concave sides. Whorls convex with the rounded periphery just above the suture, last whorl half-way evenly rounded from suture to umbilicus. Whorls channeled below the suture. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into slight, evenly spaced riblets. Spiral sculpture on the last whorl: 1 fine and inconspicuous to distinct, narrow thread at the periphery; above the periphery 1–2 similar well-spaced threads, below the periphery 2–4 more, including the basal thread, umbilical impression without threads, first half of penultimate whorl with 2–3 threads, the lowermost close to the suture; shell locally also with (traces of) a fine striation. Aperture: Peristome thickened, double, the inner a thin to thick rim which often slightly protrudes from the outer; the outer peristome white, (widely) spreading and gradually narrowing in the umbilical region. Dimensions. Height 10.8–15.0 mm; width 11.5–15 mm; ratio height/width 0.94–1.01; diameters of the first 3 whorls 0.70–0.90 mm, 1.4–1.5 mm, 2.4–2.6 mm respectively; umbilicus 1.4–1.8 mm wide, 11–13 % of the shell width; number of whorls 5 1/8–6 1/8; height aperture 5.8–9.0 mm; width aperture 6.5–8.5 mm. Periostracum thin, deciduous, with short, thin hairs where radial riblets cross spiral sculpture.

Distribution in Sabah. Scattered localities in E; elsewhere rare: Balambangan island, mount Tambuyukon. Elevation range: 0–800 m. Primary and secondary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Genus Leptopoma L Pfeiffer, 1847

Diagnosis for the Sabah species. Shell medium-sized: 10–24 mm wide. Spire conical. Spiral keel(s) or threads present. Aperture without a notch in the inner peristome where the palatal peristome meets the body whorl, inside without a pore close to the aperture, outside in the same place without a tubule. Periostracum very thin, smooth. Operculum thin, corneous.

Notes. 1. See Phung et al. (2017b) for a morphological and molecular phylogenetic analysis of the Sabah species.

2. See also *Cyclostoma tenebricosum* A Adams & Reeve under Species of Uncertain Position, and *Leptopoma signatum* L Pfeiffer under Excluded species.

KEY TO THE GROUPS

1 - Last whorl keeled, with only inconspicuous spiral sculpture above and below

- Group 1
- 1 Last whorl rounded to moderately angular at the periphery; if moderately angular then with distinct spiral threads above and below **Group 2**

Group 1

Leptopoma undatum (Metcalfe, 1852)

(fig. 30e-f, 31a-c, map 4d)

Pfeiffer 1851e: 146; 1852b: 113; 1852c: 18; 1858: 75; Reeve 1862a: Pl. 4, fig. 21; Wallace 1865: 413; Issel 1874: 427; Pfeiffer 1876: 133; Godwin-Austen 1889: 337; Kobelt 1906 (1902–1908): 456; Laidlaw 1937: 186; Saul 1967: 109; Vermeulen 1996b: 284; 1999: 148; Schilthuizen & Rutjes 2001: 420; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Phung et al. 2017b: 2. — Cyclostoma undatum Metcalfe 1852 (1851): 71. — Leptopoma (Trocholeptopoma) undatum (Metcalfe) Kobelt & Von Möllendorff 1897c: 81; Kobelt 1902: 31; Zilch 1954: 53; Marzuki et al. 2021: 17. — Type from 'Borneo'.

Leptopoma skertchlyi Smith 1895: 119. – Leptopoma (Trocholeptopoma) skertchlyi (Smith) Kobelt & Von Möllendorff 1897c: 81; Kobelt 1902: 30; Von Martens 1908: 255. – Type from Malaysia, Sabah, 'mount Ambun'.

Description. Shell medium-sized, rather thin, white with patchy, translucent banding parallel to the growth lines, rarely with some oblique, zig-zag, pale brown lines. Surface somewhat shiny. Spire conical. Whorls: First two whorls convex, other whorls flat, last whorl at the periphery with a sharp, slightly pinched keel that abruptly changes into a more inconspicuous edge in the last 1/3-1/4 whorl, thus disrupting the regular curvature of the keel when the shell is observed from below, last whorl almost flat above and below the periphery. Sculpture. Radial sculpture: Inconspicuous growth lines. Spiral sculpture: Fine striation combined with up to 7 inconspicuous, slightly raised threads above the periphery. Dimensions. Height 14–21 mm; width 14–24 mm; ratio height/width 0.78-0.91; number of whorls 5 3/4-6 1/2; height aperture 7–12 mm; width aperture 8–15 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2400 m. In primary or secondary forest, tolerant to lowland kerangas forest and peat swamp forest on acid soils, also in plantations, coastal shrubland, sand dunes. On various bedrock types, lives on vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Philippines.

Variability. Variable in size and the ratio height/width. In some thick-shelled specimens the peripheral keel on the last whorl is shallowly and obtusely serrate.

Group 2

Leptopoma atricapillum (G B Sowerby I, 1843)

(fig. 30g, 31d-e, map 4d)

Pfeiffer 1847: 109; 1851e: 146; 1852b: 115; 1852c: 18; 1858: 76; Reeve 1862a: Pl. 1, fig. 6; Von Martens 1867: 150; Pfeiffer 1876: 134; Kobelt 1886: 50; Dohrn 1889: 57; Von Möllendorff 1894: 214; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017b: 2. – *Cyclostoma atricapillum* G B Sowerby I 1843a: 137; 1843b: 64. – *Leptopoma (Trocholeptopoma) atricapillum* (G B Sowerby I) Kobelt & Von Möllendorff 1897c: 80; Kobelt 1902: 19; Zilch 1954: 147. – Type from Philippines, Mindoro, Calapan.

Cross diagnosis. Differs from *Leptopoma sericatum* by having a slightly more elongated spire, and by the large number of spiral threads below the periphery. The radial sculpture is also coarser. Juveniles may resemble *Japonia jucunda* but differ by the presence of distinct spiral sculpture below the periphery.

Description. Shell medium-sized, rather thin, white to pale brownish, often with brown spiral bands, interrupted by zig-zag oblique brown lines and patches. Surface shiny. Spire conical. Whorls moderately convex, rounded, last whorl convex, rounded, at the periphery rounded to somewhat obtusely angular. Sculpture. Radial sculpture: Growth lines, locally grading into well-spaced, fine riblets. Spiral sculpture: Periphery with a distinct thread; above the periphery with 4–5 such threads, below the periphery with 14–20 threads, the basal one usually the most distinct, then grading to finer threads in the umbilical impression; next to these fine, densely placed spiral striation present. Dimensions. Height 12–14 mm; width 10.5–13 mm, ratio height/width 1.09–1.18, shell wider than high; number of whorls 5 3/8–5 3/4; height aperture 5.5–6.7 mm; width aperture 5.6–7.1 mm.

Distribution in Sabah. Scattered localities in SE: Silam Coast Conservation Area, Tun Sakaran Marine Park. Elevation range: 0–300 m. In coastal woodland on limestone and volcanic soil. Distribution elsewhere: Philippines, including the Sulu Archipelago.

Leptopoma perlucidum (Grateloup, 1840)

(fig. 31h–j, map 4e)

Pfeiffer 1847: 108; 1851d: 144; 1852b: 103; 1852c 17; 1858: 70 ('pellucidum'); Reeve 1862a: Pl. 5, fig. 27 ('pellucidum'); 1876: 128 ('pellucidum'); Kobelt & Von Möllendorff 1897c: 79; Van Benthem Jutting 1959: 60; Maassen 1997: 35; 2001: 18; Vermeulen 1999: 152 ('pellucidum'); Schilthuizen & Vermeulen 2003a: 95 ('pellucidum'); Schilthuizen et al. 2003b: 41 ('pellucidum'); Schilthuizen 2004: 94 ('pellucidum'); Clements et al. 2008: 2761 ('pellucidum'); Liew et al. 2010: Online Supporting Information, Appendix S1 ('pellucidum'); Schilthuizen et al. 2011: 4 ('pellucidum'); Schilthuizen et al. 2013: Online supplementary data ('pellucidum'); Phung et al. 2017: 58 ('pellucidum'); Phung et al. 2017b: 2 ('pellucidum'); Uchida et al. 2013: 52, 53 ('pellucidum'); Foon et al. 2018: 96 ('pellucidum'). – Cyclostoma perlucidum Grateloup 1840: 169. – Type from Philippines, Manilla.

Cyclostoma nitidum G B Sowerby I in Reeve 1842 (1841–1842): Pl. 183, fig. 2; 1843a: 33; 1843b: 60. – Leptopoma nitidum (G B Sowerby I) Saul 1967: 109. – Type from Philippines.

Leptopoma lowi Pfeiffer 1855c: 210; 1858: 70; Von Martens 1867: 149; Issel 1874: 426; Pfeiffer 1876: 128; Aldrich 1889: 25; Godwin-Austen 1889: 336; Kobelt & Von Möllendorff 1897c: 79; Kobelt 1902: 11; 1906 (1902–1908): 464; Von Martens 1908: 255; Zilch 1954: 143. – Type from Borneo, 'Labuan island'.

Description. Shell medium-sized, rather thin, white to pale brown, often with translucent banding parallel to the growth lines and/or the spiral sculpture, with or without (dark) brown spiral bands, if present often combined with color patterns following the growth lines. Surface shiny. Spire conical. Whorls moderately convex, rounded, the last whorl convex, well-rounded, or slightly more narrowly rounded at the periphery. Sculpture. Radial sculpture: Inconspicuous growth lines. Spiral sculpture: Periphery with or without an inconspicuous thread; above the periphery sometimes with up to 5, even weaker threads, sometimes with one more below the periphery; next to these a fine striation present. Dimensions. Height 10–16 mm; width 10–16 mm, ratio height/width 0.97–1.10, but shell often slightly higher than wide; number of whorls 5–5 1/2; height aperture 5.8–9.2 mm; width aperture 6.2–9.5 mm.

Distribution in Sabah. Widespread, common, but not deep inland. Elevation range: 0–2400 m. In forest on limestone bedrock. Lives on the forest floor and on vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Uncertain; similar forms occur from Taiwan to Indonesia (Sumatra) to Papua New Guinea.

Variability. An unresolved species complex, extreme variability occurs in size, spiral sculpture, and coloration.

Leptopoma sericatum (L Pfeiffer, 1851)

(fig. 30e-f, 31h-j, map 4f)

Pfeiffer 1851e: 145; 1852b: 108; 1852c: 17; 1858: 72; Reeve 1862a: Pl. 5, fig. 26; Von Martens 1867: 149; Issel 1874: 426; Pfeiffer 1876: 131; Aldrich 1889: 25; Godwin-Austen 1889: 336; Schepman 1896: 157; Von Martens 1908: 278; Saul 1967: 109; Vermeulen 1996b: 284; 1999: 154; Schilthuizen & Rutjes 2001: 420; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Phung et al. 2017b: 2; Foon et al. 2018: 96; Marzuki et al. 2021: 17. – Cyclostoma (Leptopoma) sericatum Pfeiffer 1851a: 244. – Leptopoma (Trocholeptopoma) sericatum (L Pfeiffer) Kobelt & Von Möllendorff 1897c: 81; Kobelt 1902: 30; Von Martens 1908: 255. – Type from 'Borneo'.

Cross diagnosis. Differs mainly from *Leptopoma perlucidum* by the stronger spiral sculpture. Intermediate specimens do occur, but rarely so.

Description. Shell medium-sized, rather thin, white to pale brownish, often with translucent banding parallel to the spiral sculpture, often with yellowish, orange, pinkish brown to dark brown spiral bands, less commonly combined with color patterns following the growth lines. Surface shiny. Spire conical. Whorls moderately convex, rounded; the last convex, rounded to somewhat obtusely angular at the periphery rounded above and below. Sculpture. Radial sculpture: Inconspicuous growth lines. Spiral sculpture: Periphery usually with a moderately distinct thread; above the periphery with 3–6 such threads, below the periphery with 1–2(–6); next to these a fine striation present. Dimensions. Height 9–15 mm; width 9–15.5 mm, ratio height/width 0.92–1.05, but shell often slightly wider than high; number of whorls 4 3/8–5 1/8; height aperture 5.0–8.0 mm; width aperture 5.0–9.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1700 m. In primary and secondary forest, also in roadside vegetation. Lives on the floor and on vegetation. On various bedrock types. Also in Sarawak, Kalimantan. Distribution elsewhere: Uncertain; similar forms occur in Indonesia (Sumatra, Java), Philippines.

Genus Opisthoporus Benson, 1851

Diagnosis for the Sabah species. Shell medium-sized to large: 11–29 mm wide. Spire almost flat to slightly raised. No prominent spiral sculpture. Aperture with a (slight) notch in the inner peristome where the palatal peristome meets the body whorl; with a pore in the inner surface, close to the aperture and the suture, which passes through the shell wall and on the outer shell surface emerges as a fold or a tubule near the suture which is closed or open at the end. Periostracum rather thin, smooth. Operculum thick, with a calcareous layer.

Opisthoporus iris (Godwin-Austen, 1889)

(fig. 33a–d, 36a–b, map 5a)

Kobelt & Von Möllendorff 1897b: 119; Saul 1967: 110; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – Rhiostoma iris Godwin-Austen 1889: 343; 1890: 245. – Cyclotus (Opisthoporus) iris (Godwin-Austen) Kobelt 1902: 215; Von Martens 1908: 256; Kobelt 1912 (1911–1914): 844; Zilch 1956: 191. – Cyclotus iris (Godwin-Austen) Sutcharit et al. 2019b: 30. – Type from 'Borneo'.

Description. Shell medium-sized to large, rather thin, opaque, white to yellow-corneous with brown blotches or zig-zag markings which (partly) fade towards the umbilical impression. Surface somewhat shiny. Spire (slightly) raised. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines, more distinct ones at well-spaced, approx. even intervals. Spiral sculpture often absent, sometimes locally present as fine, rather inconspicuous, densely placed grooves. Aperture: Peristome thickened, double, the inner a thin, porrect or slightly widened rim which often slightly protrudes from the outer, with a slight, minute notch or a closed fissure where it is closest to the body whorl; the outer peristome spreading, flat, narrow on the columellar side, increasingly wide towards the palatal side and widest where approaching the body whorl, then deeply folded inwards over a pore in the shell wall, close to the aperture and the suture, to form an antrorse, frontally closed or open tubule which is attached to the body whorl along (part of) its length. Umbilicus deep. Dimensions. Height 6.2–16.5 mm; width 11.0–29.5 mm; ratio height/width 0.41–0.64; diameters of the first 3 whorls 1.0–1.2 mm, 2.6–3.2 mm, 5.8–8.0 mm respectively; umbilicus 3.0–9.0 mm wide, 25–41 % of the shell width

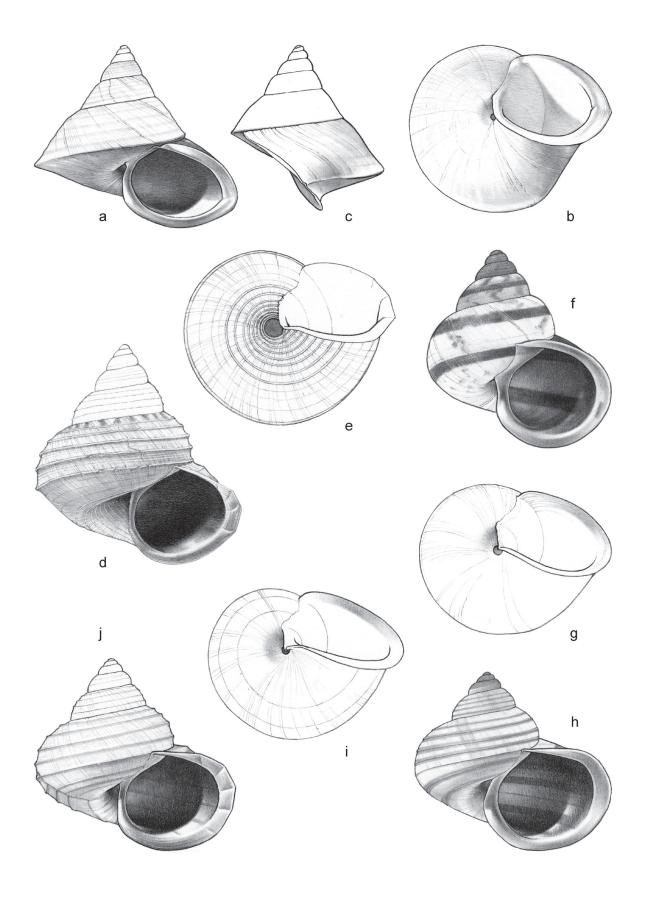


Fig. 31, a–c. *Leptopoma undatum* (Metcalfe, 1852), a. Frontal view, shell 18 mm high, b. Umbilical view, c. Right lateral view; d–e. *Leptopoma atricapillum* (G B Sowerby I, 1843), d. Frontal view, shell 14 mm high, e. Umbilical view; f–g. *Leptopoma perlucidum* (Grateloup, 1840), f. Frontal view, shell 13 mm high, g. Umbilical view; h–j. *Leptopoma sericatum* (L Pfeiffer, 1851), h. Frontal view, shell 12 mm high, i. Umbilical view, j. Frontal view, shell 13 mm high.

(measured without the peristome); number of whorls 3 5/8–4 1/2; height aperture 3.3–10.0 mm (measured over the inner peristome; width aperture 4.0–11.0 mm. Periostracum brown, thin, rather deciduous, silky, with minute folds over the growth lines, with short hairs in some specimens. Operculum outside with very slowly expanding whorls with appressed edges.

Distribution in Sabah. Widespread, common. Elevation range: 0–1800 m. Primary and secondary forest, plantations. On various bedrock types. Also in Sarawak, Kalimantan. Endemic to Borneo.

Variability. Extremely variable in size.

Opisthoporus pterocycloides (L Pfeiffer, 1855)

(fig. 32e-h, 36c, map 5b)

Pfeiffer 1858: 27; Von Martens 1867: 114; Issel 1874: 438; Pfeiffer 1876: 42; Godwin-Austen 1889: 341; Kobelt & Von Möllendorff 1897b: 119; Von Martens 1908: 274. – *Cyclostoma (Cyclotus) pterocycloides* Pfeiffer 1855 (1854a): 300. – *Pterocyclos anomalus* Reeve 1863b: Pl. 5 fig. 27. – *Cyclotus (Opisthoporus) pterocycloides* (L Pfeiffer) Kobelt 1902: 216; Von Martens 1908: 257; Kobelt 1913 (1911–1914): 970. – *Cyclotus pterocycloides* (L Pfeiffer) Sutcharit et al. 2019b: 45. – Type locality not specified.

Opisthoporus birostris auct. Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1.

[Not Cyclostoma birostre L Pfeiffer].

Cross diagnosis. Differs from *Opisthoporus iris* by the operculum with detached and raised whorl edges (as *Pterocyclos tenuilabiatus*). Shells without operculum generally differ from *O. iris* by the shallower (not wider) umbilicus, a difference best observed by comparing shells of the two species.

Description. Shell medium-sized to large, rather thin, opaque, white to yellow-corneous with brown blotches or zig-zag markings which (partly) fade towards the umbilical impression; sometimes almost entirely brown. Surface somewhat shiny. Spire slightly raised, or approx. flat with the apex slightly raised, just visible above the level of the last whorl if the shell is observed frontally. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines. Spiral sculpture rather inconspicuous, sometimes only locally present, densely placed, shallow, somewhat wavy grooves. Aperture: Peristome thickened, double, the inner a thin, porrect or slightly widened rim which often slightly protrudes from the outer, with a slight, minute notch or a closed fissure where it is closest to the body whorl; the outer peristome spreading, flat but in fully mature shells close to the edge on the palatal side often concave, narrow on the columellar side, increasingly wide towards the palatal side and widest approaching the body whorl, then deeply folded inwards over a pore in the shell wall, close to the aperture and the suture, to form an antrorse, frontally closed or open tubule which is attached to the body whorl along (part of) its length. Umbilicus rather shallow. Dimensions. Height 5.8–12.0 mm; width 15.0–26.0 mm; ratio height/width 0.36–0.50; diameters of the first 3 whorls 0.9–1.4 mm, 2.2–3.5 mm, 5.4–8.0 mm respectively; umbilicus 5.0–10.0 mm wide, 30–43 % of the shell width (measured without the peristome); number of whorls 4–4 7/8; height aperture 3.2–7.0 mm (measured over the inner peristome); width aperture 4.0–7.8 mm. Periostracum brown, thin, rather deciduous, without hairs. Operculum outside with the inner whorls very slowly expanding and the outer more rapidly, with the edge of the outer whorls detached from the next whorl.

Distribution in Sabah. Widespread, common. Elevation range: 0–1100 m. Primary and secondary forest, plantations. On various bedrock types. Also in Sarawak, Kalimantan. Endemic to Borneo.

Genus *Platyrhaphe* Von Möllendorff, 1890

Diagnosis for the Sabah species. Shell very small to medium-sized: 4.5–11.8 mm wide. Spire (low-) conical. Spiral threads present or absent. Aperture without a notch in the inner peristome where the palatal peristome meets or is closest to the body whorl, inside without a pore close to the aperture, outside in the same place without a tubule. Periostracum very thin, smooth. Operculum thick, with a calcareous layer.

Notes. The shells of living animals are thickly encrusted with soil.

Platyrhaphe bicolor (E Von Martens, 1903)

(fig. 33a–c, map 5c)

Von Martens 1908: 277. – *Cyclotus (Platyrhaphe) bicolor* Von Martens 1903: 421 ('*Platyraphe*'). – Type from Indonesia, Kalimantan, 'gunung Sekerat'.

Platyrhaphe linitus auct. Schilthuizen et al. 2003b: 42 ('*Platyraphe*'); Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

(Sp.) 'Bor-01' Uchida et al. 2013: 52, 53.

[Not Cyclotus linitus Godwin-Austen].

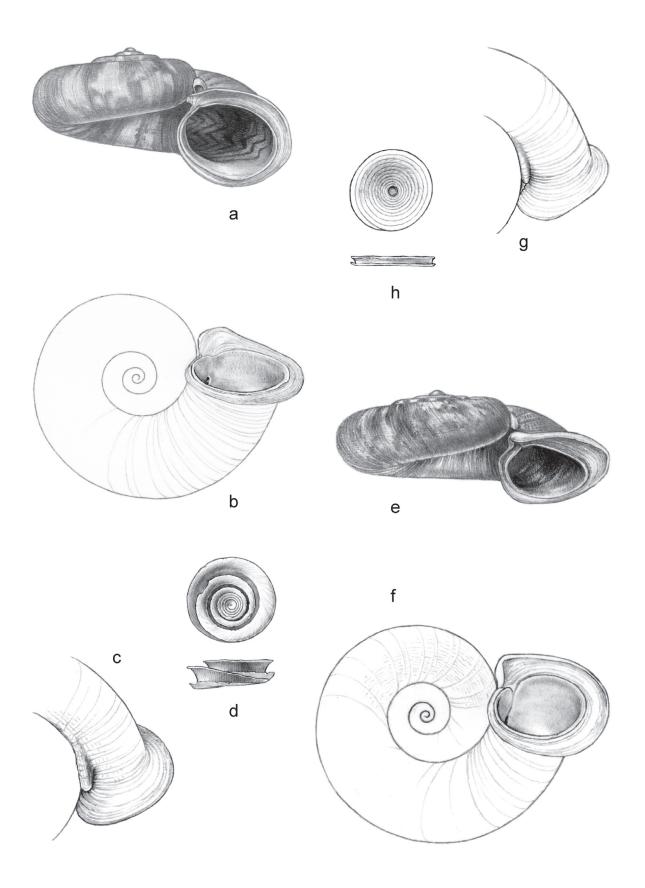


Fig. 32, a–d. *Opisthoporus iris* (Godwin-Austen, 1889), a. Frontal view, shell 8.0 mm high, b. Umbilical view, c. Apical view, part near aperture, d. Operculum, above: Outer surface, below: Lateral view; e–h. *Opisthoporus pterocycloides* (L Pfeiffer, 1855), e. Frontal view, shell 10.5 mm high, f. Umbilical view, g. Apical view, part near aperture, h. Operculum, above: Outer surface, below: Lateral view.

Description. Shell rather small, rather thin, opaque, white, apex purple or red-brown. Surface dull. Spire conical with slightly concave sides, last 1/4 whorl slightly descending and turned inwards, detached from the previous whorl. Whorls convex, evenly rounded, not channeled below the suture. Sculpture. Protoconch smooth at 40x magnification. Teleoconch. Radial sculpture: Growth lines, rather densely placed at slightly uneven intervals, locally developing into very fine, low, rounded riblets, which below the suture and in the umbilical impression are appressed, thin, and have a fragile crest. Spiral sculpture on the first 2–2 3/4 whorl only, fine, densely placed threads on the first whorl, more widely spaced, less distinct, somewhat wavy threads on the next. Aperture: Peristome slightly thickened or not, if thickened single or indistinctly double, with the inner a thin, hardly protruding rim, and the outer slightly spreading or not. Dimensions. Height 7.0–10.8 mm; width 8.6–11.8 mm; ratio height/ width 0.75–0.92; diameters of the first 3 whorls 0.8–1.0 mm, 1.8–2.3 mm, 4.0–5.2 mm respectively; umbilicus 1.8–2.8 mm wide, 19–27 % of the shell width; number of whorls 3 7/8–4 1/2; height aperture 3.5–4.6 mm; width aperture 3.8–5.2 mm.

Distribution in Sabah. Scattered localities in E. Elevation range: 0–400 m. Forest and coastal woodland on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Variability. Sabah material shows variability in size. Also, material from elsewhere is variable in relative aperture size and the height of the spire. The description is based on Sabah material only.

Platyrhaphe bongaoensis (E A Smith, 1894)

(fig. 27c-d, 33d-e, map 5c)

Kobelt & Von Möllendorff 1897b: 115; Kobelt 1902: 180; 1912 (1911–1914): 879; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 60; Foon et al. 2018: 96. – *Cyclotus bongaoensis* Smith 1894c: 57. – *Cyclotus (Platyrhaphe) bongaoensis* (E A Smith) Von Möllendorff 1894: 212. – Type from Philippines, Sulu Archipelago, Bongao.

Cross diagnosis. Distinctly smaller than *Platyrhaphe bicolor*, and with spiral sculpture from apex to aperture. Also, the umbilicus is generally wider, compared to the shell width. Juveniles may be confused with sympatric *Japonia borneensis* but differ by the almost orthocline radial sculpture and absence of color patterns.

Description. Shell small, thin, opaque, white, apex often (somewhat) red-brown. Surface dull or slightly shiny. Spire (low-)conical with concave sides, last 1/4–3/8 whorl slightly descending, slightly to distinctly turned inwards, detached from the previous whorl. Whorls convex, evenly rounded, not channeled below the suture. Sculpture. Protoconch smooth at 40x magnification. Teleoconch. Radial sculpture: Growth lines, and widely and slightly unevenly spaced, rather distinct, low, rounded ribs, most conspicuously present on the last 1–1 1/2 whorl. Spiral sculpture: Conspicuous, low, rather thin, rounded threads, well-spaced but somewhat more densely placed around the umbilical impression, and absent immediately below the suture. Aperture: Peristome not thickened, not spreading. Dimensions. Height 3.4–4.8 mm; width 4.5–7.0 mm; ratio height/width 0.64–0.91; diameters of the first 3 whorls 0.7–0.9 mm, 1.5–2.0 mm, 3.7–4.9 mm respectively; umbilicus 1.3–2.3 mm wide, 26–33 % of the shell width; number of whorls 3 1/4–3 3/4; height aperture 1.9–2.5 mm; width aperture 1.8–2.6 mm.

Distribution in Sabah. Islands in N: Mantanani, Balambangan and Banggi islands. Elevation range: 0–100 m. Coastal primary forest and shrub vegetation on limestone bedrock. Distribution elsewhere: Philippines (Sulu Archipelago).

Variability. Variable in size and, to a lesser extent, the height of the spire.

Genus *Pterocyclos* Benson, 1832

Diagnosis for the Sabah species. Shell medium-sized to large: 10–35.2 mm wide. Spire slightly concave with a raised apex to slightly raised as a whole. No prominent spiral sculpture. Aperture with or without a slight notch in the inner peristome where the palatal peristome meets the body whorl, without a pore in the inner surface, close to the aperture and the suture, on the outer shell surface with or without a fold or a tubule. Periostracum rather thin, smooth. Operculum thick, with a calcareous layer.

KEY TO THE GROUPS

- 1 Growth lines on the last whorl, just before it widens towards the aperture and close to the suture, approx. straight over a short distance or slightly to distinctly sinuous

 Group 1
- 1 Growth lines on the last whorl, just before it widens towards the aperture and close to the suture, evenly rounded Group 2

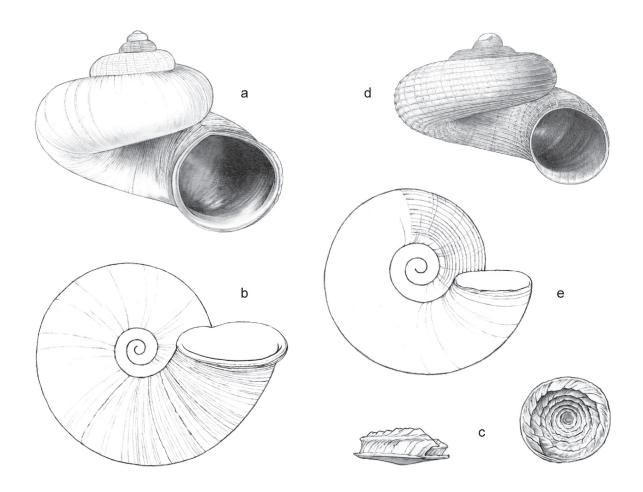


Fig. 33, a–c. *Platyrhaphe bicolor* (E Von Martens, 1903), a. Frontal view, shell 8.2 mm high, b. Umbilical view, c. Operculum, left: Lateral view, right: Outer surface; d–e. *Platyrhaphe bongaoensis* (E A Smith, 1894), d. Frontal view, shell 4.8 mm high, e. Umbilical view.

Pterocyclos boxalli (Godwin-Austen, 1893)

(fig. 34a–d, map 5d

Rhiostoma boxalli Godwin-Austen 1893: 32; Von Martens 1908: 256; Kobelt 1902: 538; Sutcharit et al. 2019b: 13. – Opisthoporus boxalli (Godwin-Austen) Vermeulen 1996b: 284. – Type from Malaysia, Sabah, 'near Kina Balu'.

[Not Cyclotus boxalli Godwin-Austen 1889: 343].

Cross diagnosis. Identified among Sabah *Pterocyclos* by the folding of the outer peristome where the palatal side meets the body whorl: With a shallow to deep fold, in some shells almost closed frontally, almost forming a tube-like structure. In apical view, this fold resembles the tubule present in *Opisthoporus*. In *Pterocyclos boxalli*, however, the fold does not start with a pore on the inner surface of the shell, as in *Opisthoporus*.

Description. Shell medium-sized to rather large, rather thin, opaque, white to yellow-corneous with (red-) brown blotches or (interrupted) zig-zag markings which (partly) fade towards the aperture and the umbilical impression. Surface somewhat shiny. Spire slightly raised to slightly concave with the apex, or the first whorls, slightly raised, just visible above the level of the last whorl if the shell is observed frontally. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines, at well-spaced, approx. even intervals more distinct than in between; radial sculpture near the aperture, close to the suture, approx. straight over a short distance or slightly to distinctly sinuous. Spiral sculpture: Fine, rather inconspicuous, often only locally present, densely placed but somewhat unevenly spaced shallow, wavy grooves. Aperture: Peristome thickened, double, the inner a thin, porrect or slightly widened rim which often slightly protrudes from the outer, with a slight, minute notch or a closed fissure where it is closest to the body whorl; the outer peristome spreading, flat, narrow on the columellar side, increasingly wide towards the palatal side and widest approaching the body whorl, then deeply notched before it widens again into a shallowly concave to sharply folded, almost

tubular structure attached on one side to the body whorl. Umbilicus deep. Dimensions. Height 8.0–11.5 mm; width 19.5–25.8 mm; ratio height/width 0.36–0.45; diameters of the first 3 whorls 1.0–1.2 mm, 2.8–3.2 mm, 6.8–8.2 mm respectively; umbilicus 5.8–8.0 mm wide, 32–35 % of the shell width (measured without the peristome); number of whorls 4–4 5/8; height aperture 5.5–8.5 mm (measured over the inner peristome; width aperture 7.5–10.0 mm. Periostracum brown, thin, rather deciduous, silky, with minute folds over the growth lines, without hairs. Operculum outside with many slowly and evenly expanding whorls with appressed whorl edges.

Distribution in Sabah. Rare in W: Highland: Kinabalu (old record), Crocker range, Trus Madi range, Pun Batu. Elevation range: 500–1700 m. Wet or dry primary forest on sandstone/shale or limestone bedrock. Also in Sarawak. Distribution elsewhere: Philippines (Palawan).

Variability. The fold where the outer peristome touches the body whorl is narrow and deep in most shells, but shallow and open in some.

Pterocyclos tenuilabiatus (Metcalfe, 1852)

(fig. 34e–h, map 5d)

Pfeiffer 1851d: 136; 1852b: 45; 1852c: 8; 1858: 28; Reeve 1863b: Pl. 1, fig. 5; Pfeiffer 1865: 41; Von Martens 1867: 114; Issel 1874: 435; Pfeiffer 1876: 50; Tenison Woods 1888: 1062; Aldrich 1889: 25; Godwin-Austen 1889: 339; Schepman 1896: 157; Kobelt & Von Möllendorff 1897b: 114; Kobelt 1902: 170; Von Martens 1908: 256; Kobelt 1911 (1911–1914): 742; Zilch 1956: 173; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Phung et al. 2017: 57; Foon et al. 2018: 96; Marzuki et al. 2021: 20. – *Cyclostoma tenuilabiatum* Metcalfe 1852 (1851): 71. – Type from 'Borneo'.

Pterocyclos labuanensis Pfeiffer 1864 (1863): 525; 1865: 41; Von Martens 1867: 115; Pfeiffer 1869 (1866–1869): 443; 1876: 50; Issel 1874: 436; Tenison Woods 1888: 1063; Godwin-Austen 1889: 339. – Cyclotus (Aulacopoma) labuanensis (L Pfeiffer) Kobelt & Von Möllendorff 1897b: 118; Kobelt 1902: 212; Von Martens 1908: 256; Kobelt 1912 (1911–1914): 823. – Cyclotus labuanensis (L Pfeiffer) Sutcharit et al. 2019: 31. – Type from Malaysia, 'Labuan island'.

Pterocyclos lowianus Pfeiffer 1864 (1863): 526; 1865: 41; Von Martens 1867: 115 ('loweanus'); Pfeiffer 1869 (1866–1869): 443; 1876: 50; Issel 1874: 435 ('loweanus'); Tenison Woods 1888: 1063; Godwin-Austen 1889: 339. – Cyclotus (Eucyclotus) lowianus (L Pfeiffer) Kobelt & Von Möllendorff 1897b: 118. – Cyclotus lowianus (L Pfeiffer) Kobelt 1902: 200; Von Martens 1908: 256; Kobelt 1911 (1911–1914): 811; Sutcharit et al. 2019: 34. – Type from Malaysia, 'Labuan island'.

Pterocyclos latilabrum Smith 1895: 116; Kobelt & Von Möllendorff 1897b: 113; Kobelt 1902: 166; Von Martens 1908: 277; Kobelt 1911 (1911–1914): 737; Zilch 1956: 172; Solem 1964: 12; Saul 1967: 110; Sutcharit et al. 2019: 33. – Type from Malaysia, Sabah, 'Gomanton Hill'.

- (?) Pterocyclos kobelti Clench & Archer 1932: 38. Type from Malaysia, Sabah, West Coast Prov., mount Kinabalu.
- (?) Pterocyclos brevis auct. Saul 1967: 110.

[Not Lituus brevis Martyn].

Cross diagnosis. Identified among Sabah *Pterocyclos* by the operculum with detached and raised whorl edges. Shells without operculum can generally be distinguished from *P. trusanensis* by the wider umbilicus, compared to the shell width (36–45 % of the shell width without the peristome, versus 27–35 %).

Description. Shell medium-sized to large, rather thin, opaque, white to yellow-corneous with brown blotches or (interrupted) zig-zag markings which (partly) fade towards the aperture and the umbilical impression; some shells almost entirely brown above the periphery. Surface somewhat shiny. Spire slightly raised with approx. straight sides, to almost flat with only the apex visible above the level of the last whorl if the shell is observed frontally. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines, at well-spaced, approx. even intervals more distinct than in between; radial sculpture near the aperture, close to the suture, approx. straight over a short distance or slightly to distinctly sinuous. Spiral sculpture: Fine, (rather) inconspicuous, densely placed but somewhat unevenly spaced shallow, wavy grooves, often most conspicuously present on the penultimate whorl, sometimes approx. absent on the outer. Aperture: Peristome thickened, double, the inner a thin, porrect or slightly spreading rim which (slightly) protrudes from the outer, usually with a shallow notch where it is closest to the body whorl; the outer peristome slightly to widely spreading, flat with the outer edge often concave, narrow on the columellar side, wider towards the palatal side, widest and shaped into an obtusely triangular, concave wing when approaching the body whorl, with one side of the triangle attached to the body whorl. Dimensions. Height 5.0–15.0 mm; width 11.2–31.0 mm; ratio height/width 0.38–0.53; diameters of the first 3 whorls 1.0-1.3 mm, 2.2-3.1 mm, 5.2-8.0 mm respectively; umbilicus 4-10.2 mm wide, 36-45 % of the shell width (measured without the peristome); number of whorls 3 3/4-4 7/8; height aperture

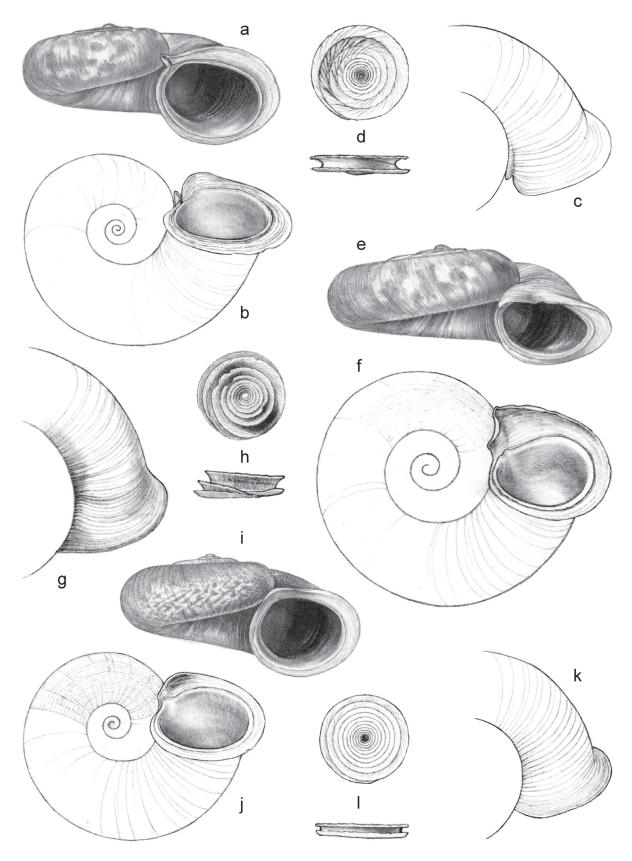


Fig. 34, a–d. *Pterocyclos boxalli* (Godwin-Austen, 1893), a. Frontal view, shell 10 mm high, b. Umbilical view, c. Apical view, part near aperture, d. Operculum, above: Outer surface, below: Lateral view; e–h. *Pterocyclos tenuilabiatus* (Metcalfe, 1852), e. Frontal view, shell 7.8 mm high, f. Umbilical view, g. Apical view, part near aperture, h. Operculum, above: Outer surface, below: Lateral view; i–l. *Pterocyclos trusanensis* (Godwin-Austen, 1889), i. Frontal view, shell 7.0 mm high, j. Umbilical view, k. Apical view, part near aperture, l. Operculum, above: Outer surface, below: Lateral view.

2.8–7.5 mm (measured over the inner peristome; width aperture 3.3–10.0 mm. Periostracum brown, thin, rather deciduous, rather dull or with a silky sheen, without hairs. Operculum outside with slowly expanding whorls, with the edge of the outer whorls detached from the next whorl.

Distribution in Sabah. Widespread, common. Elevation range: 0–1000 m. Primary forest, coastal forest, secondary forest on limestone or volcanic bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Variable in size. Some populations in the lower Kinabatangan river valley (including the type of the junior subjective synonym *Pterocyclos latilabrum*) and along Tabin river are characterized by a widely flaring outer peristome.

Pterocyclos trusanensis (Godwin-Austen, 1889)

(fig. 34i–l, 36d–e, map 5e)

Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96. – *Cyclotus trusanensis* Godwin-Austen 1889: 344; Kobelt 1902: 203; Von Martens 1908: 256; Kobelt 1912 (1911–1914): 833; Solem 1964: 13; Sutcharit 2019b: 53. – *Cyclotus (Eucyclotus) trusanensis* (Godwin-Austen) Kobelt & Von Möllendorff 1897b: 118. – Type from Malaysia, Sarawak, 'Trusan island'.

[Not *Pterocyclos trusanensis* auct. Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94; = *Pterocyclos variegatus*].

Cross diagnosis. Particularly resembles *Pterocyclos variegatus*; in addition to the character in the key below the genus description, *P. trusanensis* usually differs by the more open coiling (diameter of the third whorl 7.8–9.5 mm versus 6.4–8.0 mm), and by the presence of at least traces of spiral sculpture on the shell surface.

Description. Shell medium-sized, rather thin, opaque, yellow-corneous with pale brown blotches or (interrupted) zig-zag markings which (partly) fade towards the aperture and the umbilical impression. Surface somewhat shiny. Spire slightly raised, just visible above the level of the last whorl if the shell is observed frontally. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines, at well-spaced, approx. even intervals more distinct than in between; radial sculpture near the aperture, close to the suture, approx. straight over a short distance, or slightly to distinctly sinuous. Spiral sculpture: Fine, (rather) inconspicuous, densely placed but somewhat unevenly spaced shallow, wavy grooves, only locally present in some shells. Aperture: Peristome thickened, double, the inner a thin, porrect or slightly spreading rim which slightly protrudes from the outer or not, approx. without a notch where it is closest to the body whorl; the outer peristome moderately spreading, flat, narrow on the columellar side, somewhat wider towards the palatal side, widest and somewhat concave when approaching the body whorl. Dimensions. Height 7.2-9.0 mm; width 15.0-20.0 mm; ratio height/width 0.42–0.53; diameters of the first 3 whorls 1.0–1.5 mm, 3.0–3.8 mm, 7.8–9.5 mm respectively; umbilicus 3.8-6.0 mm wide, 27-35 % of the shell width (measured without the peristome); number of whorls 3 3/4-4; height aperture 5.0-5.5 mm (measured over the inner peristome; width aperture 6.0-7.0 mm. Periostracum brown, thin, rather deciduous, silky, without hairs. Operculum outside with very slowly expanding whorls with appressed whorl edges.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Trus Madi range. Elevation range: 900–2700 m. Wet primary forest on sandstone/shale and diorite bedrock. Also in Sarawak. Endemic to Borneo.

Note. We assume that the type locality 'Trusan island' is Trusan, Sarawak rather than Terusan, Sabah, because the collector, Everett, was Resident of the former.

Group 2

Pterocyclos fraterculus Vermeulen & Liew, new species

(fig. 35a-c, map 5d)

Type specimens from Malaysia, Sabah, Pinangah river valley, Batu Urun (holotype BOR/MOL 14646; paratypes JV 1136/>50 shells).

Cross diagnosis. Differs from *Pterocyclos variegatus* by its distinctly smaller size, and more slowly expanding whorls (third whorl 4.8–5.7 mm diameter, versus 6.4–8.0 mm).

Description. Shell medium-sized, rather thick, opaque, white to yellow-corneous with (pale) brown, approx. transverse blotches which often turn into zig-zag markings below the periphery. Surface shiny. Spire slightly raised with concave sides. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Densely placed, somewhat raised growth lines; radial sculpture near the aperture, close to the suture, evenly rounded. Spiral sculpture: Locally traces of very fine, densely placed, shallow grooves, cutting into the raised parts of the growth lines; radial sculpture near the aperture and close to the suture evenly rounded. Aperture: Peristome

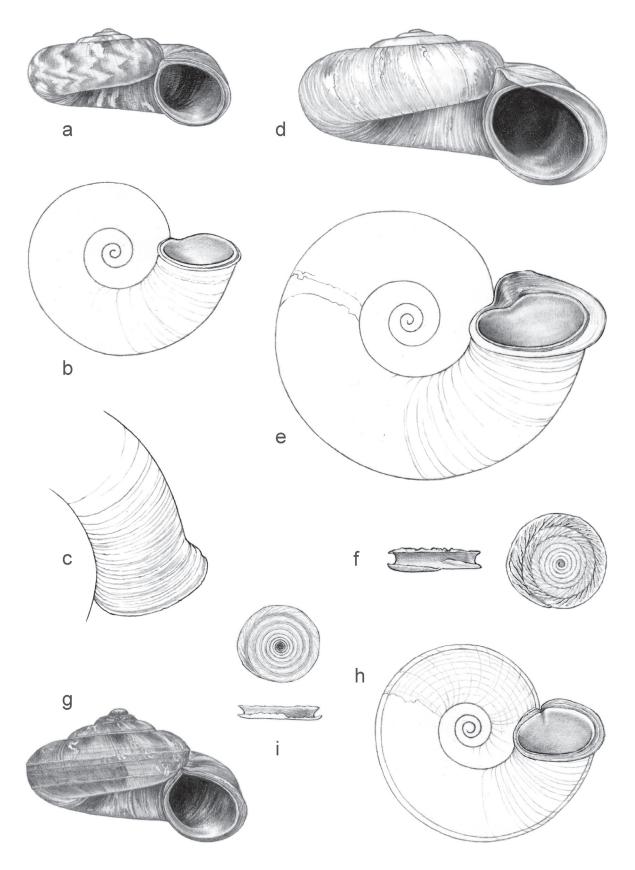


Fig. 35, a–c. *Pterocyclos fraterculus* Vermeulen & Liew, new species, a. Frontal view, shell 5.2 mm high, b. Umbilical view, c. Apical view, part near aperture; d–f. *Pterocyclos variegatus* (Swainson, 1840), d. Frontal view, shell 15 mm high, e. Umbilical view, f. Operculum, left: Lateral view, right: Outer surface; g–i. *Scabrina serpentinitica* Vermeulen & Liew, new species, g. Frontal view, shell 6.4 mm high, h. Umbilical view, i. Operculum, above: Outer surface, below: Lateral view.

thickened, double, the inner a thin, porrect rim which slightly protrudes from the outer, approx. without a notch where it is closest to the body whorl; the outer peristome slightly spreading, concave, narrow on the columellar side, slightly wider towards the palatal side, widest, but still narrow and without a wing, and less concave or flat when approaching the body whorl. Dimensions. Height 4.8–6.5 mm; width 10.0–13.5 mm; ratio height/width 0.42–0.55; diameters of the first 3 whorls 0.9–1.1 mm, 2.0–2.5 mm, 4.8–5.7 mm respectively; umbilicus 3.2–5.3 mm wide, 32–41 % of the shell width (measured without the peristome); number of whorls 3 7/8–4 1/4; height aperture 3.0–4.0 mm (measured over the inner peristome); width aperture 3.2–4.5 mm.

Distribution in Sabah. Sinobang only. Elevation range: 300–400 m. Primary forest on limestone bedrock. Endemic to Sabah.

Note. Although abundant in number of shells, our material does not provide information about the periostracum and operculum.

Name derivation. From fraterculus (Latin) = little brother.

Pterocyclos variegatus (Swainson, 1840)

(fig. 35d–f, 36f, map 5f)

Cyclotus variegatus Swainson 1840: 336; Pfeiffer 1851d: 135; 1852b: 39; 1852c: 7; 1858: 25; Reeve 1863a: Pl. 6, fig. 29; Pfeiffer 1865: 33; Smith 1894c: 56; Kobelt 1902: 203; 1911 (1911–1914): 793; Zilch 1956: 187. – Cyclotus (Eucyclotus) variegatus (Godwin-Austen) Von Möllendorff 1894: 212; Kobelt & Von Möllendorff 1897b: 118. – Type from Philippines, Sulu islands.

Cyclotus euzonus Dohrn 1889: 54; Smith 1893a: 352; Kobelt 1902: 198; 1911 (1911–1914): 801; Zilch 1956: 185. – Cyclotus (Eucyclotus) euzonus (Dohrn) Kobelt & Von Möllendorff 1897b: 117; Kobelt 1902: 198. – Type from Philippines, 'Paragua'.

Cyclotus (Eucyclotus) amabilis Fulton 1905: 93; Von Martens 1908: 256. – Pterocyclos amabilis (Fulton) Schilthuizen 2004: 94; Liew et al. 2010: Online Supporting Information, Appendix S1; Phung et al. 2017: 57. – Cyclotus amabilis (Fulton) Sutcharit et al. 2019: 5. – Type from Malaysia, 'N. Borneo'.

Pterocyclos trusanensis auct. Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94.

[Not Pterocyclos trusanensis (Godwin-Austen)].

Description. Shell large, rather thick, opaque, white to cream-yellow to pale corneous, with or without brown markings: A transverse, pale brown marbling to transverse, narrow zig-zag bands, sometimes interrupted by a darker brown spiral band, or a strip of white around the periphery; some specimens with 1-2 dark brown spiral bands only. Surface shiny. Spire slightly raised with approx. straight or slightly concave sides. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Densely placed, somewhat raised growth lines; radial sculpture near the aperture, close to the suture, evenly rounded. Spiral sculpture absent, in some specimens seemingly present because of the presence of minute indentations in the crest of the more prominent growth lines. Aperture: Peristome thickened, double, the inner a thin, porrect rim which slightly protrudes from the outer, with or without a notch where it is closest to the body whorl; the outer peristome spreading, concave, narrow on the columellar side, distinctly wider towards the palatal side, widest and shaped into an obtusely triangular, concave wing when approaching the body whorl, with one side of the triangle (partly) attached to the body whorl. Dimensions. Height 9.0-15.1 mm; width 20.8-35.2 mm; ratio height/width 0.39-0.49; diameters of the first 3 whorls 1.2–1.5 mm, 2.8–3.5 mm, 6.4–8.0 mm respectively; umbilicus 7.0–13.2 mm wide, 29–42 % of the shell width (measured without the peristome); number of whorls 4 1/2-5 1/4; height aperture 5.5-9.2 mm (measured over the inner peristome; width aperture 6.8–11.1 mm. Periostracum ochre-yellow to olive-green, thin, rather deciduous, silky, over the growth lines with minute folds with densely placed short hairs on the crest. Operculum outside with appressed whorl edges.

Distribution in Sabah. Widespread, common. Elevation range: 0–1500 m. Primary and secondary forest, coastal forest on limestone bedrock; sometimes persistent after severe degradation. Also in Sarawak, Kalimantan. Distribution elsewhere: Philippines (Palawan, Sulu Archipelago).

Variability. Many Sabah populations have shells without any brown markings. On the islands Banggi and Balambangan the form with one or more spiral color bands occurs (for instance, the type of the junior subjective synonym Cyclotus euzonus), next to marbled specimens.

Genus Scabrina W T Blanford, 1863

Diagnosis for the Sabah species. Shell medium-sized: 10.8–12 mm wide. Spire low-conical. Spiral threads present. Aperture with a notch in the inner peristome where the palatal peristome meets the body whorl, inside



Fig. 36, a-b. *Opisthoporus iris* (Godwin-Austen, 1889); c. *Opisthoporus pterocycloides* (L Pfeiffer, 1855); d-e. *Pterocyclos trusanensis* (Godwin-Austen, 1889); f. *Pterocyclos variegatus* (Swainson, 1840).

without a pore close to the aperture, outside in the same place without a tubule. Periostracum rather thin, with scales over the most prominent spiral threads. Operculum thick, with a calcareous layer.

Note. Inclusion of the species below in *Scabrina* is based on overall similarity with *S. brounae* (Sykes, 1898), as well as on its low-conical spire and prominent spiral sculpture which morphologically sets it apart from Borneo *Pterocyclos*, with which it would key out otherwise.

Scabrina serpentinitica Vermeulen & Liew, new species

(fig. 35g–i, map 6a)

Type specimens from Malaysia, Sabah, Meliau range, E of Solonsong river, N of Telupid (holotype BOR/MOL 14847; paratype JV 13533/1 shell).

Cross diagnosis. Shells without operculum resemble *Japonia* species, particularly *J. borneensis* (*Japonia* Group 4), but are larger (shell width 10.8–12.0 mm, versus width 5.5–7.7 mm), have a less distinct spiral sculpture, and a dull shell surface.

Description. Shell medium-sized, thin, opaque, corneous to ochre-brown with dark brown transverse blotches above the periphery. Surface approx. dull. Spire low-conical with slightly concave sides. Whorls convex, last whorl evenly rounded from suture to umbilicus. Sculpture. Radial sculpture: Somewhat raised growth lines, at well-spaced, approx. even intervals slightly more distinct than in between. Spiral sculpture: 2 rather distinct, low, rounded spiral threads, one above and one below the periphery; in between these 2-7 finer threads, above the upper 4-7 finer threads, and below the lower 1-3, all with still finer spiral striation in between; no spiral threads in the umbilical impression. Aperture: Peristome thickened, double, the inner a thin, porrect rim which hardly protrudes from the outer, with a shallow notch where it reaches the body whorl from the palatal side; outer peristome somewhat spreading, flat, narrow on the columellar side, somewhat wider towards the palatal side, widest when approaching the body whorl. Dimensions. Height 6.4-7.0 mm; width 10.8-12.0 mm; ratio height/width 0.59-0.60; diameters of the first 3 whorls c. 0.8 mm, 1.4-1.7 mm, 2.8-3.7 mm respectively; umbilicus 3.6-4.0 mm wide, c. 34 % of the shell width (measured without the peristome); number of whorls 5–5 1/2; height aperture 3.0–3.8 mm (measured over the inner peristome; width aperture 3.8-4.8 mm. Periostracum brown, thin, rather persistent, with rows of short, antrorsely appressed hairs over the most prominent growth lines, and with much longer, upright hairs where these cross the two most prominent spiral threads. Operculum outside with slowly expanding whorls, with appressed whorl edges.

Distribution in Sabah. Meliau range only. Elevation range: 100–200 m. Primary forest on serpentinite bedrock. Endemic to Sabah.

Similar species elsewhere. Resembles Scabrina brounae (Sykes, 1898) and S. liratula (Preston, 1909), both from Sri Lanka; S. serpentinitica differs by the less rapidly expanding whorls and, as a consequence, by the smaller aperture, as well as by the less distinct spiral sculpture above the periphery on the last whorl.

Name derivation. From the rock type serpentinite, the bed rock of the type locality.

Family **DIPLOMMATINIDAE** L Pfeiffer, 1856

Diagnosis for the Sabah species. Shell dextral or sinistral, minute to small, cylindrical, ellipsoid, ovoid or conical; last part of the last whorl sometimes detached. Constriction present, usually in the last whorl or in the last part of the penultimate whorl, rarely higher up in the spire, without a pore in the inner surface, close to the suture. Color white to orange(-red). Sculpture usually consisting of radial ribs, often with subordinate spiral striation. Aperture without teeth, or with a parietal tooth, rarely with more than 1 tooth. Peristome thickened, spreading, inner on the palatal and/or basal side with or without a lip parallel to the margin (see fig. 37c). Umbilicus closed or open. Operculum corneous or calcareous, circular, with few whorls; nucleus central.

Notes. 1. Measurements of the shell are taken as follows (see also fig. 6):

The **whorl count**: Includes the tuba in the genera *Arinia*, *Diplommatina* and *Moussonia*, but excludes the tuba in the genera *Opisthostoma* and *Plectostoma*.

The **diameter of the umbilicus**: Maximum diameter of the space encircled by the last whorl, but excluding the last, deviating portion of the spire (the tuba, or part of it).

The **shell height**: Includes the peristome; the shell width, however, is measured over the widest whorl, but excludes the spreading part of the peristome.

The **aperture size** is the size over the actual opening. The peristome is excluded.

2. When identifying material, it is advisable to check a series of specimens if possible. Identifying single specimens leads to less reliable results.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Tuba coiled around an axis which forms a clear angle with the axis of the spire
 - 2 Spire (excluding tuba) with 3–3 3/4 whorls
 - 2 Spire (excluding tuba) with 4 5/8–7 1/2 whorls
- 1 Tuba coiled around an axis which runs approx. parallel to the axis of the spire

Genus *Opisthostoma*Genus *Plectostoma*

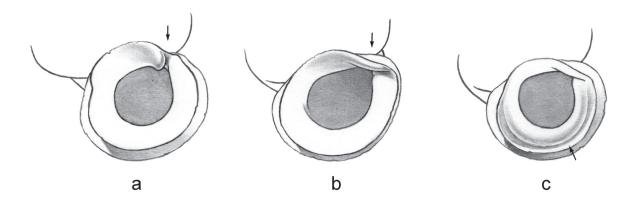


Fig. 37, a–c. Explanatory figures with *Arinia*; a. Inner peristome just above the angular edge with a fold oblique or perpendicular to the margin of the peristome (see arrow); b. Inner peristome just above the angular edge with a protrusion approx. parallel to the margin of the peristome (see arrow); c. Inner peristome wih a lip parallel to the margin on the palatal and basal side (see arrow).

3 – Aperture without a columellar tooth (a furrow may be present)

Genus Arinia

- 3 Either aperture with a columellar tooth, or aperture without a columellar tooth, but then tuba with an indistinct columellar lamella
 - 4 Aperture tilted up to 30° relative to the coiling axis of the spire

Genus Diplommatina

4 – Aperture tilted 45–60° relative to the coiling axis of the spire

Genus Moussonia

Genus Arinia H & A Adams, 1856

Diagnosis for the Sabah species. Shell white. Tuba coiled around an axis which runs approx. parallel to the axis of the spire. Tuba without a columellar lamella. Aperture not or hardly tilted downwards relative to the coiling axis of the spire. Spire 4–5 3/8(–5 5/8) whorls, including a tuba of 1/4–3/4(–1 1/4) whorls.

KEY TO THE GROUPS

- 1 Inner peristome just above the upper corner with a fold oblique or perpendicular to the margin of the peristome (see fig. 37a)
 - 2 Penultimate whorl with double-crested ribs (single-crested ribs may also be present)

Group 3

- 2 Penultimate whorl with single-crested ribs only
 - 3 Umbilicus closed, or umbilicus open, 0.05–0.1 mm wide

Group 1

3 – Umbilicus open, 0.15–0.25 mm wide

Group 2

- 1 Inner peristome just above the upper corner: Either a) with a fold approx. parallel to the margin of the peristome (see fig. 37b), or b) with a fold or knob of unclear orientation to the margin of the peristome, or c) without fold, knob, or protrusion
 - 4 Penultimate whorl with some or many double-crested ribs (single-crested ribs may also be present)

Group 6

- 4 Penultimate whorl with single-crested ribs only
 - 5 Umbilicus open, deep (penultimate whorl open), 0.05–0.30 mm wide

Group 4

5 – Umbilicus closed, or umbilicus rimate, or umbilicus open but shallow (penultimate whorl closed), up to 0.10 mm wide Group 5

Group 1

Check also:

Arinia turgida (Group 5). Shells with a fold in the inner peristome, just above the upper corner, which is oblique or perpendicular to its margin, are characterized within Group 1 by the palatal peristome which distinctly protrudes beyond the penultimate whorl.

Arinia boreoborneensis Vermeulen, 1996

(fig. 38a–c, map 6b)

Vermeulen 1996a: 98; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

Cross diagnosis. Distinguished within Group 1 by the absence of radial ribs above the aperture, on the ultimate whorl. Some shells of *Arinia clausa* have inconspicuous radial ribs above the aperture, but they are never entirely absent.

Description. Shell shortly fusiform, (pen-)ultimate whorl widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 4–14 ribs/0.5 mm, on the penultimate whorl absent or 3–5 ribs/0.5 mm, ribs absent above the aperture. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side at most slightly protruding beyond the penultimate whorl, columellar side not or hardly sinuous; outer peristome at most somewhat spreading beyond the inner on the palatal and basal side, (slightly widened and then) rather gradually narrowed on the columellar side, gradually narrowed towards the upper corner; inner peristome often fused to the outer just above the upper corner, with an inconspicuous to distinct ridge oblique or perpendicular to the margin, at the right side of which a furrow, palatal and basal side without a lip. Dimensions. Height 1.45–1.80 mm; width 0.80–0.90 mm; ratio height/width 1.8–2.1; umbilicus 0.05–0.10 mm wide; number of whorls 4 1/4–4 3/4, including a tuba of slightly less than 3/8 whorl; height aperture 0.35–0.45 mm; width 0.35–0.40 mm.

Distribution in Sabah. Rare in N: Kudat (old record), Balambangan and Banggi islands. Elevation: 0 m. In (coastal) woodland on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. Kudat specimens differ from those from Banggi island in often having a penultimate whorl partly without ribs, a more inconspicuous ridge near the upper corner of the aperture, and a slightly more protruding inner peristome.

Arinia clausa Vermeulen, 1996

(fig. 38h–j, map 6b)

Vermeulen 1996a: 99; Schilthuizen 2004: 94; Clements et al. 2008: 2761. – Type from Sarawak, 4th Div., Gunung Mulu N.P., near National Park entrance.

Cross diagnosis. Differs from *Arinia cylindrica cylindrica* by the more gradually narrowing peristome on the columellar side and towards the upper corner. Also, the spire is usually less strictly cylindrical. Differs from *A. cylindrica crassilabris* by the inner peristome without a poorly demarcated lip on the palatal and basal side.

Description. Shell approx. shortly cylindrical, or shortly fusiform, last two whorls widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 8–18 ribs/0.5 mm, on the penultimate whorl 5–10 ribs/0.5 mm, above the aperture sometimes inconspicuous but still visible, 5–8 ribs/0.5 mm. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side at most moderately protruding beyond the penultimate whorl, columellar side somewhat sinuous or not; outer peristome hardly to moderately spreading beyond the inner on the palatal and basal side, gradually narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with an inconspicuous to distinct ridge oblique to the margin, at the right side of which a furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.40–1.90 mm; width 0.85–1.05 mm; ratio height/width 1.5–2.1; umbilicus closed but rimate in oblique view, or open, up to 0.05 mm wide; number of whorls 4 1/8–5, including a tuba of c. 3/8 whorl; height and width aperture 0.35–0.45 mm.

Distribution in Sabah. Widespread in W but rare: Pulau Tiga Park, Crocker range. Elevation range: 0–700 m. Disturbed primary forest, coastal forest on limestone bedrock. Also in Sarawak and Kalimantan. Endemic to Borneo

Variability. The radial ribs above the aperture may be inconspicuous in some specimens, but are always visible, not absent as in Arinia boreoborneensis.

Note. The identity of the Tiga island population is somewhat uncertain; the shells resemble sympatric *A. insularum* (Group 4) except for the character given in the key to the groups.

Arinia cylindrica cylindrica Vermeulen, 1996

(fig. 38d–f, map 6c)

Vermeulen 1996a: 99; Schilthuizen 2004: 94; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Differs from *Arinia boreoborneensis* and *A. clausa* by the rather abruptly narrowing of the outer peristome on the columellar side. It also has a slightly longer tuba and less convex whorls.

Description. Shell cylindrical, last two whorls widest. Whorls moderately convex. Sculpture. Radial ribs single-crested, on the apical whorls 10–22 ribs/0.5 mm, on the penultimate whorl 10–20 ribs/0.5 mm, above the aperture 6–10 ribs/0.5 mm. Spiral striation absent, sometimes present but fine and very inconspicuous. Aperture not

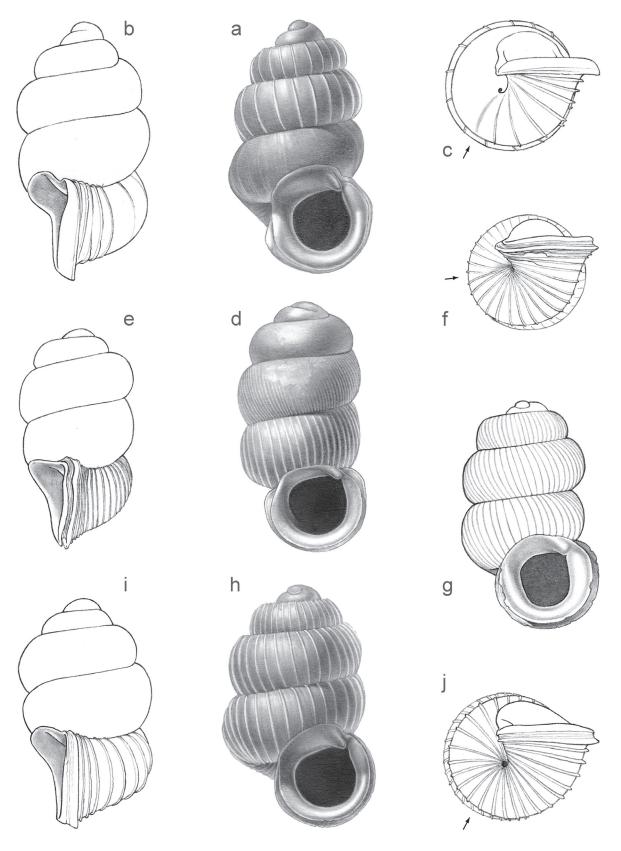


Fig. 38, a–c. *Arinia boreoborneensis* Vermeulen, 1996, a. Frontal view, shell 1.8 mm high, b. Right lateral view, c. Umbilical view, arrow indicates constriction; d–f. *Arinia cylindrica cylindrica* Vermeulen, 1996, d. Frontal view, shell 1.9 mm high, e. Right lateral view, f. Umbilical view, arrow indicates constriction; g. *Arinia cylindrica crassilabris* Vermeulen, 1996, g. Frontal view, shell 1.6 mm high; h–j. *Arinia clausa* Vermeulen, 1996, h. Frontal view, shell 1.6 mm high, i. Right lateral view, j. Umbilical view, arrow indicates constriction.

turned upwards. Peristome: Palatal side not or hardly protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome somewhat spreading beyond the inner or not on the palatal and basal side, (slightly widened and then) rather abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a rather inconspicuous to a distinct ridge oblique to the margin, at the right side of which a furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.45–1.80 mm; width 0.75–0.90 mm; ratio height/width 1.8–2.2; umbilicus closed but rimate in oblique view; number of whorls 4 1/4–5 1/8, including a tuba of slightly more than 3/8 whorl; height and width aperture 0.30–0.40 mm.

Distribution in Sabah. Widespread, scattered localities: Balambangan and Banggi islands, Crocker range, lower Kinabatangan. Elevation range: 0–700 m. Disturbed primary forest and coastal dry primary forest on limestone bedrock. Endemic to Sabah.

Arinia cylindrica crassilabris Vermeulen, 1996

(fig. 38g, map 6c)

Vermeulen 1996a: 99. – Type from Malaysia, Sabah, Sandakan Prov., limestone hill 7 miles E of Lamag, 3 miles NNW of Laab, near road Lahad Datu-Sandakan, near Kinabatangan river.

Cross diagnosis. Morphologically intermediate between *Arinia cylindrica cylindrica* and *A. clausa* in the length of the tuba; it differs from these two taxa by the presence of a lip on the inner peristome.

Description. As the nominate subspecies, but shell (shortly) cylindrical. Aperture: Inner peristome on the palatal and basal side with a rather poorly demarcated lip parallel to the margin. Dimensions. Height 1.60–1.75 mm; width 0.80–0.90 mm; ratio height/width 1.9–2.0; number of whorls 4 1/2–4 5/8, including a tuba of (slightly less than) 3/8 whorl; height and width aperture 0.30–0.40 mm.

Distribution in Sabah. Rare in E: Lower Kinabatangan, Silam Coast Conservation Area. Elevation range: 0–100 m. In (disturbed) primary forest and coastal forest on limestone bedrock. Endemic to Sabah.

Group 2

Arinia biplicata Vermeulen, 1996

(fig. 39a–d, map 6b)

Vermeulen 1996a: 100; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Characterized among Borneo *Arinia* by the furrow inside the tuba, on the columellar side, bordered by two longitudinal ridges towards the constriction.

Description. Shell shortly cylindrical to shortly fusiform, last whorl or last two whorls widest. Whorls moderately convex. Constriction with two high longitudinal ridges, a parietalis and a basalis, both continuing into the tuba and gradually disappearing towards the aperture. Sculpture. Radial ribs single-crested, on the apical whorls and the penultimate whorl 16–22 ribs/0.5 mm, above the aperture 3–6 ribs/0.5 mm. Spiral striation absent or present, fine and inconspicuous. Aperture not turned upwards, with the basal ridge just visible inside. Peristome: Palatal side not protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome slightly to moderately spreading beyond the inner on the palatal and basal side, rather abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a ridge oblique to the margin, at the right side of which an inconspicuous furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.20–1.40 mm; width 0.70–0.85 mm; ratio height/width 1.5–1.7; umbilicus 0.15–0.20 mm wide; number of whorls 4–4 1/2, including a tuba of about 3/8–1/2 whorl; height and width aperture 0.25–0.30 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In disturbed primary forest on limestone bedrock. Endemic to Sabah.

Arinia borneensis E A Smith, 1893

(fig. 39e–g, map 6d)

Smith 1893b: 350; Vermeulen 1996a: 102; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data. – *Arinia (Leucarinia) borneensis* (Smith) Kobelt & Von Möllendorff 1898: 131; Kobelt 1902: 391; Von Martens 1908: 257. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Arinia inexpectans Solem 1964: 16. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

[Not Arinia borneensis auct. Phung et al. 2017: 63; = Arinia insularum].

Description. Shell shortly fusiform, last whorl widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 6–14 ribs/0.5 mm, on the penultimate whorl 6–8 ribs/0.5 mm, above the aperture 4–6 ribs/0.5

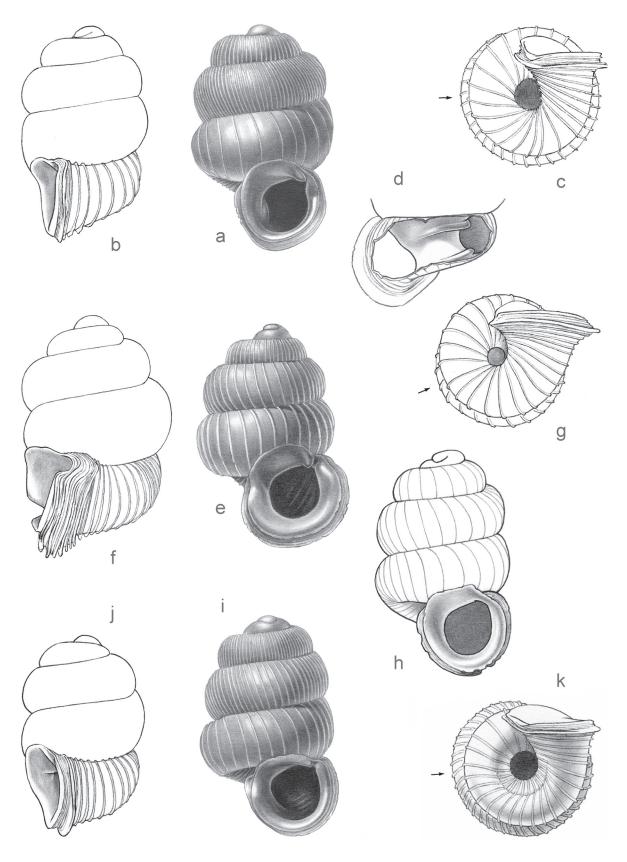


Fig. 39, a–d. *Arinia biplicata* Vermeulen, 1996, a. Frontal view, shell 1.3 mm high, b. Right lateral view, c. Umbilical view, arrow indicates constriction, d. Back view, part of the shell removed to show internal structure; e–g. *Arinia borneensis* E A Smith, 1893, e. Frontal view, shell 1.8 mm high, f. Right lateral view, g. Umbilical view, arrow indicates constriction; h–k. *Arinia pertusa* Vermeulen, 1996, h. Frontal view, shell 1.6 mm high, i. Frontal view, shell 1.6 mm high, j. Right lateral view, k. Umbilical view, arrow indicates constriction.

mm. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side slightly to moderately protruding beyond the penultimate whorl, columellar side often somewhat sinuous; outer peristome usually moderately spreading beyond the inner on the palatal and basal side, rather gradually narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a ridge oblique to the margin, at the right side of which a distinct furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.60–2.45 mm; width 1.00–1.45 mm; ratio height/width 1.5–1.8; umbilicus 0.15–0.20 mm wide; number of whorls 4 1/4–4 7/8, including a tuba of 3/8–1/2 whorl; height and width aperture 0.4–0.5 mm.

Distribution in Sabah. Widespread, scattered localities, common in lower Kinabatangan. Elevation range: 0–1200 m. Primary and secondary forest on limestone and sandstone/shale bedrock. Also in Kalimantan. Endemic to Borneo.

Arinia pertusa Vermeulen, 1996

(fig. 39h–k, map 6e)

Vermeulen 1996a: 101; Clements et al. 2008: 2761. – Type from Sabah, Tawau Prov., Baturong-Madai F.R., Madai hill, 40 km SSW of Lahad Datu.

Cross diagnosis. Among Borneo Arinia it is generally characterized by its wide umbilicus. Differs from A. borneensis by the outer peristome which abruptly narrows on the columellar side and towards the upper corner. Specimens without a fold in the upper corner of the peristome key out in Group 4, see under A. simplex and A. oviformis.

Description. Shell shortly cylindrical to shortly fusiform, last whorl or last two whorls widest. Whorls (moderately) convex. Sculpture. Radial ribs single-crested, on the apical whorls 4–20 ribs/0.5 mm, on the penultimate whorl 5–18 ribs/0.5 mm, above the aperture 4–12 ribs/0.5 mm. Spiral striation absent, rarely present on the apical whorls, fine. Aperture not turned upwards. Peristome: Palatal side not or hardly protruding beyond the penultimate whorl, columellar side not or hardly sinuous; outer peristome slightly to moderately spreading beyond the inner on the palatal and basal side, slightly widened and then abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with or without a ridge oblique to the margin, at the right side of which a furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.30–1.85 mm; width 0.75–1.00 mm; ratio height/width 1.5–1.9; umbilicus 0.15–0.25 mm wide; number of whorls 4 1/8–5, including a tuba of 3/8–1/2 whorl; height aperture 0.35–0.45 mm; width 0.30–0.40 mm.

Distribution in Sabah. Rare in E: Lower Kinabatangan, Ulu Segama, Baturong-Madai; elsewhere in Sapulut only, there common. Elevation range: 0–500 m. In primary and secondary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Regional forms can be distinguished:

Form A (fig. 39i–k). Tuba usually 1/2 whorl. Radial ribs densely placed, moderately spaced above the aperture. Angular ridge present.

Distribution in Sabah. Baturong-Madai.

Includes the type specimen.

Form B. Tuba (slightly more than) 3/8 whorl. Radial ribs densely placed. Angular ridge absent.

Distribution in Sabah. Baturong-Madai.

The morphological partition between the two Madai hill forms is almost perfect, but some specimens are intermediate.

Form C (fig. 39h). Tuba 3/8–1/2 whorl. Radial ribs widely spaced (Gomantong hill) or rather densely placed (Lamag-Laab area). Angular ridge absent.

Distribution in Sabah. Lower Kinabatangan.

Form D. Tuba 3/8 whorl. Radial ribs densely placed, moderately spaced above the aperture. Angular ridge present, sometimes small.

Distribution in Sabah. Sapulut.

Sympatric Arinia oviformis has a very shortly fusiform shell and lacks the ridge in the upper corner.

Group 3

Arinia paricostata Vermeulen, 1996

(fig. 40a-c, map 6f)

Vermeulen 1996a: 112; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256, 257; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 94; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong, 50 km WSW of Lahad Datu.

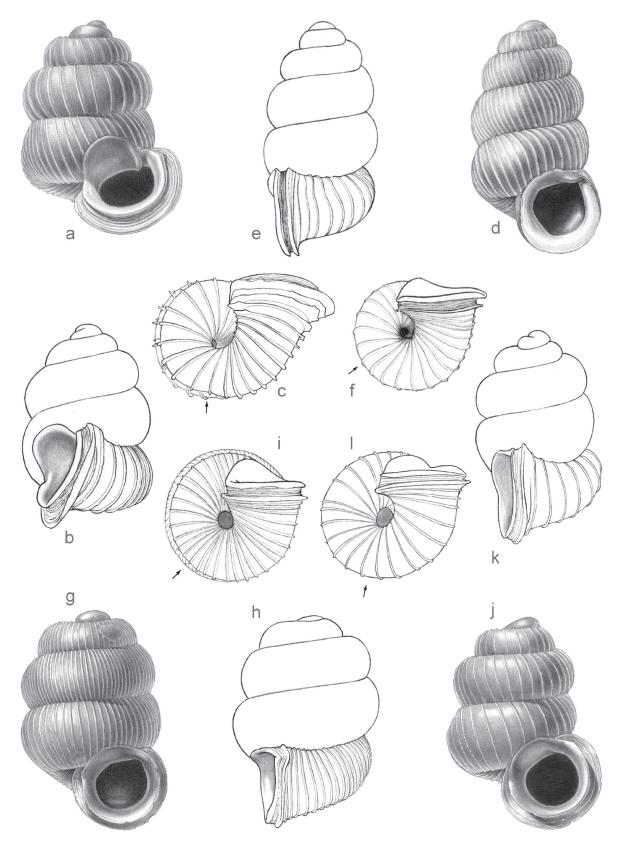


Fig. 40, a–c. *Arinia paricostata* Vermeulen, 1996, a. Frontal view, shell 2.1 mm high, b. Right lateral view, c. Umbilical view, arrow indicates constriction; d–f. *Arinia insularum* Vermeulen & Liew, new species, d. Frontal view, shell 2.0 mm high, e. Right lateral view, f. Umbilical view, arrow indicates constriction; g–i. *Arinia oviformis* Vermeulen, 1996, g. Frontal view, shell 1.7 mm high, h. Right lateral view, i. Umbilical view, arrow indicates constriction; j–l. *Arinia simplex* Vermeulen, 1996, j. Frontal view, shell 1.7 mm high, k. Right lateral view, l. Umbilical view, arrow indicates constriction.

Description. Shell conical with (slightly) convex sides, or approx. (shortly) cylindrical, last whorl widest. Whorls convex, last whorl moderately convex. Sculpture. Radial ribs double-crested with the distal crest highest, but on the last c. 1 1/4 whorl and sometimes close to the apex single-crested, on the apical whorls 6–12 ribs/0.5 mm, on the penultimate whorl 3–8 ribs/0.5 mm, above the aperture 4–8 ribs/0.5 mm. Spiral striation fine. Aperture turned slightly to distinctly upwards. Peristome: Palatal side distinctly protruding beyond the penultimate whorl, columellar side sinuous or not; outer peristome moderately to widely spreading beyond the inner on the palatal and basal side, (rather) abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a ridge oblique or perpendicular to the margin, at the right side of which a distinct furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.65–2.50 mm; width 1.20–1.40 mm; ratio height/width 1.4–2.0; umbilicus almost closed to open, up to 0.20 mm wide; number of whorls 4 1/8–5 1/8, including a tuba of 1/4 whorl; height aperture 0.40–0.50 mm; width 0.40–0.60 mm.

Distribution in Sabah. Widespread, scattered localities, more common in E, not in N. Elevation range: 0–600 m. Primary and secondary forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. Shells are often more conical and have a wider umbilicus than the one illustrated.

Group 4

Check also:

Arinia pertusa (Group 2). See cross diagnosis with A. oviformis and A. simplex.

Arinia insularum Vermeulen & Liew, new species

(fig. 40d–f, map 6c)

Type specimens from Malaysia, Sabah, Kota Belud, Usukan island (holotype BOR/MOL 12048); Malaysia, Sabah, West Coast Province, Tiga island in Kimanis bay (paratypes JV 11351/>50 shells). *Arinia borneensis* auct. Phung et al. 2017: 63.

[Not *Arinia borneensis* E A Smith].

Cross diagnosis. Within Group 4, characterized by the outer peristome which not or hardly protrudes beyond the inner on the palatal side, and by the complete absence of spiral striation. It is also characterized by the whorl count (4 1/2–5 3/8 whorls, versus 4 1/4–4 1/2 whorls), by the generally larger size (shell height 1.75–2.30 mm, versus 1.6–1.8 mm), and by the generally slenderer shell (ratio height/width 1.8–2.1, versus 1.4–1.8).

Description. Shell conical with convex sides to shortly fusiform, almost shortly cylindrical, last two whorls widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 8–13 ribs/0.5 mm, on the penultimate whorl 7–9 ribs/0.5 mm, above the aperture 4–7 ribs/0.5 mm. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome not or hardly spreading beyond the inner on the palatal and basal side, abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a ridge approx. parallel to the margin, at the right side of which a furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.75–2.30 mm; width 0.90–1.10 mm; ratio height/width 1.8–2.1; umbilicus 0.05–0.15 mm wide; number of whorls 4 1/2–5 3/8, including a tuba of about c. 3/8 whorl or slightly shorter; height aperture 0.40–0.45 mm, width aperture 0.35–0.50 mm.

Distribution in Sabah. Islands in W: Labuan Marine Park, Pulau Tiga Park, W Coast Islands, Mantanani Islands. Elevation range: 0–100 m. In coastal woodland on limestone bedrock. Endemic to Sabah.

Note. The population on Tiga island resembles *Arinia clausa* (Group 1), apart from the character given in the key to the groups.

Name derivation. From insularum (Latin) = from the islands.

Arinia oviformis Vermeulen, 1996

(fig. 40g-i, map 7a)

Vermeulen 1996a: 107. – Type from Malaysia, Sabah, Interior Prov., 1 km SE of Simatuoh, 10 km ESE of Sapulut.

Cross diagnosis. Differs from *Arinia simplex* by the wider umbilicus (0.15–0.30 mm wide, versus c. 0.1 mm wide), and by the palatal peristome which does not or hardly protrude beyond the penultimate whorl. Differs from shells of *A. pertusa* (Group 2) without a fold in the inner peristome, just above the upper corner, by the presence of fine spiral striation (usually absent in *A. pertusa*, rarely present on the apical whorls).

Description. Shell shortly fusiform, almost shortly cylindrical, last whorl widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 12–14 ribs/0.5 mm, on the penultimate whorl 10–16 ribs/0.5 mm, above the aperture 6–12 ribs/0.5 mm. Spiral striation present, fine. Aperture not turned upwards. Peristome: Palatal side not or hardly protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome some-

what spreading beyond the inner on the palatal and basal side, abruptly narrowed or approx. truncated on the columellar side and towards the upper corner; inner peristome in the upper corner without protrusion or ridge, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.65–1.80 mm; width 1.10–1.15 mm; ratio height/width 1.4–1.6; umbilicus 0.15–0.20 mm wide; number of whorls 4 3/8–4 1/2, including a tuba of about 3/8 whorl; height and width aperture 0.40–0.45 mm.

Distribution in Sabah. Widespread but rare: Sapulut, lower Kinabatangan. Elevation range: 0–500 m. In (disturbed) primary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Arinia simplex Vermeulen, 1996

(fig. 40j–l, map 7b)

Vermeulen 1996a: 105; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Clearly different from sympatric *Arinia turgida* at Gomantong hill (see also illustrated specimens). However, populations of *A. turgida* elsewhere may approach *A. simplex* in shape; diagnostic is the depth of the umbilicus: Shallow in *A. turgida*, deep in *A. simplex*. Differs from specimens of *A. pertusa* (Group 2) without a fold in the inner peristome, just above the upper corner, by the lateral peristome which distinctly protrudes beyond the penultimate whorl and gradually narrows towards the parietal side.

Description. Shell conical with distinctly convex sides, or shortly cylindrical, last whorl widest. Whorls convex. Sculpture. Radial ribs single-crested, close to the apex 5–6 ribs/0.5 mm, on the penultimate whorl 6–7 ribs/0.5 mm, above the aperture 4–5 ribs/ 0.5 mm. Spiral striation present, fine and inconspicuous. Aperture not turned upwards. Peristome: Palatal side protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome (moderately) spreading beyond the inner on the palatal and basal side, rather gradually narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with or without a slight knob, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.6–1.7 mm; width 0.95–1.10 mm; ratio height/width 1.4–1.8; umbilicus open, deep, 0.10 mm wide, at least 0.10 mm wide at the level of the penultimate whorl; number of whorls 4 1/4, including a tuba of 1/4 whorl; height aperture 0.40–0.45 mm; width c. 0.4 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In (disturbed) forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Group 5

Arinia stenotrochus stenotrochus Vermeulen, 1996

(fig. 41a–f, map 7a)

Vermeulen 1996a: 109; Schilthuizen et al. 2002: 256, 257; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41, 42; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Foon et al. 2018: 96. – Type from Malaysia, Sarawak, 4th Div., Vrong hill, Beluru area SW of Marudi.

Description. Shell (shortly) cylindrical to shortly fusiform, last whorl widest. Whorls (moderately) convex. Sculpture. Radial ribs single-crested, on the apical whorls 12–32 ribs/0.5 mm, on the penultimate whorl 8–36 ribs/0.5 mm, above the aperture absent or up to 20 ribs/0.5 mm. Spiral striation absent, rarely present on part of the last whorl, fine, inconspicuous. Aperture not turned upwards. Peristome: Palatal side not or hardly protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome slightly spreading beyond the inner on the palatal and basal side, rather abruptly to rather gradually narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with or without a protrusion about parallel to the margin, palatal side below this protrusion with or without a transverse furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.0–1.7 mm; width 0.5–1.0 mm; ratio height/width 1.6–2.2; umbilicus closed but rimate in oblique view, or open, up to 0.10 mm wide; number of whorls 4 1/8–5, including a tuba of 1/4–1/2(–3/4) whorl; height and width aperture 0.20–0.40 mm.

Distribution in Sabah. Widespread, scattered localities, rather common in lower Kinabatangan. Elevation range: 0–1100 m. Primary and secondary forest, coastal woodland; all records from vegetation on limestone bedrock. Also in Sarawak, Kalimantan (S and E parts). Endemic to Borneo.

Variability. An extremely variable species complex. Distinct forms occur regionally, while morphological intermediates occur elsewhere. Vermeulen (1996) distinguishes three subspecies, leaving some intermediate series of shells. Sabah material covers only part of the morphological range of the subspecies (Shell cylindrical, with 4 1/4–5 whorls; tuba c. 1/2 whorl; ultimate whorl above the aperture usually with 8–20 radial ribs/0.5 mm; radial ribs

sometimes very inconspicuous; umbilicus closed; inner peristome moderately protruding from the outer, without a protrusion above the upper corner), with only few morphological intermediates between the subspecies.

Arinia stenotrochus pachystoma Vermeulen, 1996

(fig. 41g–i, map 7b)

Vermeulen 1996a: 110; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2761. – Type from Malaysia, Sarawak, 4th Div., Gunung Mulu N.P.

Arinia sp. Phung et al. 2017: 63.

Cross diagnosis. The Sabah material of the subspecies differs from the nominate subspecies by the longer tuba (5/8–3/4 whorl versus c. 1/2 whorl).

Description. As the nominate subspecies, but shell (shortly) cylindrical. Whorls (moderately) convex. Sculpture. Radial ribs single-crested, on the apical whorls 18–24 ribs/0.5 mm, on the penultimate whorl 10–32 ribs/0.5 mm, above the aperture absent or up to 16 ribs/0.5 mm. Spiral striation absent. Aperture slightly turned upwards or not. Outer peristome slightly spreading beyond the inner on the palatal and basal side. Dimensions. Height 1.20–1.95 mm; width 0.65–1.05 mm; ratio height/width 1.7–2.3; number of whorls 4 1/8–5 1/8, including a tuba of 5/8–3/4 whorl; height and width aperture 0.25–0.50 mm.

Distribution in Sabah. Widespread but rare: Crocker range, lower Kinabatangan, Tabin. Elevation range: 0–600 m. In primary and (young and species-poor) secondary lowland forest, wet montane forest; all records from vegetation on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Variability. 1. Sabah material covers only part of the morphological range of the subspecies (Shell [narrowly] cylindrical, with 4 3/4–5 1/8 whorls; ultimate whorl above the aperture and, in most specimens, the penultimate whorl, without radial ribs; umbilicus closed; inner peristome moderately protruding from the outer, without a protrusion above the upper corner).

2. Some Sabah shells are larger than the material included in Vermeulen (1996a).

Arinia stenotrochus anisopleuron Vermeulen, 1996

(fig. 41j-m, map 7b)

Vermeulen 1996a: 111; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256 ('Arianta'). – Type from Indonesia, Kalimantan Timur, Gunung Melihat.

Cross diagnosis. The Sabah material of the subspecies differs from both other subspecies by the presence of double-crested radial ribs, and by the shortly ellipsoid spire. It also differs from subsp. *pachystoma* by the shorter tuba (1/4–3/8 whorl versus 5/8–3/4 whorl).

Description. As the nominate subspecies, but shell shortly ellipsoid. Whorls convex. Sculpture. Radial ribs on the last two whorls double-crested, but single-crested above the aperture and on the first whorls, on the apical whorls 12–24 ribs/0.5 mm, on the penultimate whorl 4–14 ribs/0.5 mm, above the aperture absent or up to 4 ribs/0.5 mm. Spiral striation absent. Aperture slightly turned upwards or not. Outer peristome slightly spreading beyond the inner on the palatal and basal side. Dimensions. Height 1.20–1.85 mm; width 0.70–1.05 mm; ratio height/width 1.7–2.3; number of whorls 3 7/8–4 1/2, including a tuba of 1/4–3/8 whorl; height and width aperture 0.25–0.5 mm.

Distribution in Sabah. Danum valley only. Elevation: c. 300 m. In primary forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. The limited Sabah material is larger than material included in Vermeulen (1996a).

Arinia turgida Vermeulen, 1996

(fig. 42a-d, map 7c)

Vermeulen 1996a: 104; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data. – Type from Malaysia, Tawau Prov., Segarong hills 25 km ESE of Kunak, Batu Tengar.

Cross diagnosis. Differs from *Arinia stenotrochus* by the peristome which distinctly protrudes beyond the penultimate whorl on the palatal side. Specimens with a fold in the inner peristome oblique or perpendicular to its margin, just above the upper corner key out in Group 1, see there.

Description. Shell conical with (moderately) convex sides, or shortly cylindrical, last whorl widest. Whorls convex. Sculpture. Radial ribs single-crested, on the apical whorls 4–12 ribs/0.5 mm, on the penultimate whorl 6–14 ribs/0.5 mm, above the aperture 4–8 ribs/0.5 mm. Spiral striation absent or fine, inconspicuous. Aperture turned slightly upwards or not. Peristome: Palatal side distinctly protruding beyond the penultimate whorl, columellar side sinuous or not; outer peristome slightly to moderately spreading beyond the inner on the palatal and basal side, rather gradually narrowed on the columellar side and towards the upper corner; inner peristome just

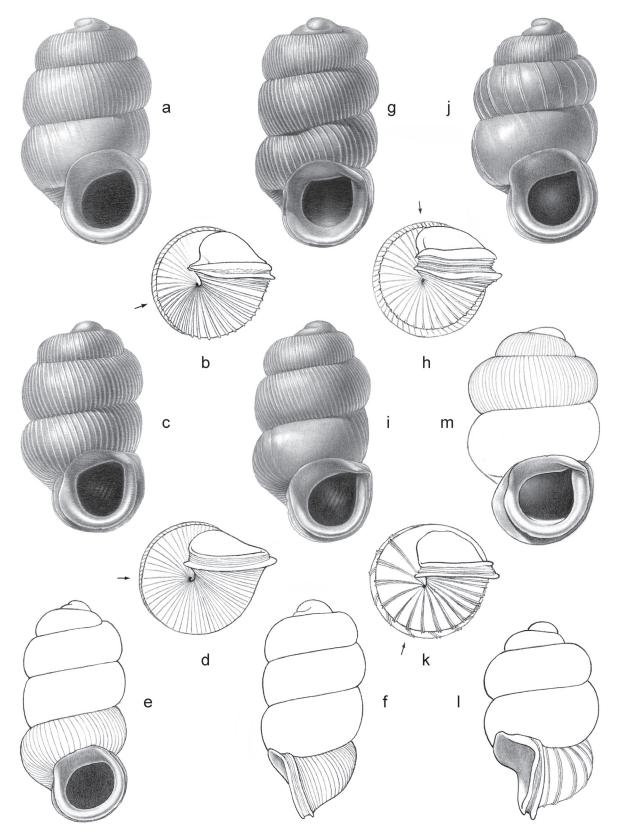


Fig. 41, a–f. *Arinia stenotrochus stenotrochus* Vermeulen, 1996, a. Frontal view, shell 1.4 mm high, b. Umbilical view, arrow indicates constriction, c. Frontal view, shell 1.2 mm high, d. Umbilical view, arrow indicates constriction, e. Frontal view, shell 1.3 mm high, f. Right lateral view; g–i. *Arinia stenotrochus pachystoma* Vermeulen, 1996, g. Frontal view, shell 1.6 mm high, h. Umbilical view, arrow indicates constriction, i. Frontal view, shell 1.5 mm high; j–m. *Arinia stenotrochus anisopleuron* Vermeulen, 1996, j. Frontal view, shell 1.5 mm high, k. Umbilical view, arrow indicates constriction, l. Right lateral view, m. Frontal view, shell 1.4 mm high.

above the upper corner with or without a knob, or a ridge oblique or perpendicular to the margin, at the right side of which often an inconspicuous furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.40–2.25 mm; width 0.85–1.40 mm; ratio height/width 1.5–1.8; umbilicus closed, or open but shallow, less than 0.10 mm wide, at most 0.05 mm wide at the level of the penultimate whorl; number of whorls 4 1/8–5, including a tuba of 1/4–3/8 whorl; height and width aperture 0.35–0.55 mm.

Distribution in Sabah. Rather common in E; elsewhere scattered localities; not in N. Elevation range: 0–1100 m. In (disturbed) primary lowland forest, dry shrubland, in wet montane forest along a stream; all records from vegetation on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Group 6

Arinia brevispira brevispira Vermeulen, 1996

(fig. 43a-b, map 7d)

Vermeulen 1996a: 115; Schilthuizen et al. 2003b: 41, 42; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Interior Prov., 5.5 km NNE of Simatuoh, 9 km E of Sapulut.

Description. Shell shortly cylindrical, last two whorls widest. Whorls convex. Sculpture. Radial ribs close to the apex single-crested, 11–15 ribs/0.5 mm, others double-crested with both crests equally high, on the penultimate whorl 5–8 ribs/0.5 mm, above the aperture with 3–5 ribs/0.5 mm, a few ribs close to the peristome single-crested again. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side at most slightly protruding beyond the penultimate whorl, columellar side moderately sinuous or not; outer peristome hardly to moderately spreading beyond the inner on the palatal and basal side, abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a (slight) protrusion about parallel to the margin, palatal side below this protrusion with a distinct transverse furrow, palatal and basal side with at most a poorly demarcated lip parallel to the margin. Dimensions. Height 1.9–2.0 mm; width 1.1–1.2 mm; ratio height/width 1.6–1.8; umbilicus 0.10–0.15 mm wide; number of whorls 4 3/8–4 5/8, including a tuba of 3/8–1/2 whorl; height and width aperture 0.45–0.50 mm.

Distribution in Sabah: Widespread but rare: Sinobang, Sapulut, lower Kinabatangan. Elevation range: 0–500 m. In (logged or otherwise disturbed) primary forest, in a damp doline; on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. In some shells of both subspecies, the columellar surface inside the aperture, behind the peristome, is somewhat convex. Such shells may resemble *Arinia streptaxiformis* but differ by the peristome which at most only slightly protrudes beyond the penultimate whorl (usually distinctly so in *A. streptaxiformis*), and by the narrower umbilicus (0.10–0.25 mm diameter versus 0.25–0.65 mm).

Arinia brevispira orientalis Vermeulen, 1996

(fig. 43c, map 7e)

Vermeulen 1996a: 115; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Tawau Prov., 'Kirk's Cave', 8 km N of Lahad Datu.

Arinia similis auct. Schilthuizen et al. 2013: Online supplementary data. [Not *Arinia similis* E A Smith].

Description. As the nominate subspecies, but last whorl (moderately) convex above the periphery, and somewhat flattened below. Sculpture. Radial ribs double-crested on the penultimate whorl, but towards the ultimate whorl and on the tuba single-crested again. Dimensions. Height 1.35–2.10 mm; width 0.95–1.20 mm; ratio height/width1.4–1.8; umbilicus 0.15–0.25 mm wide; height and width aperture 0.35–0.50 mm.

Distribution in Sabah. Scattered localities in E: Segama valley and further S. Elevation range: 0–200 m. In (disturbed) primary forest and secondary forest, in coastal vegetation, on limestone and volcanic bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. On average, Tabin specimens are slightly smaller, have a shorter and wider shell, and a wider umbilicus, than specimens near Lahad Datu.

Arinia dentifera Vermeulen, 1996

(fig. 43d–f, map 7f)

Vermeulen 1996a: 113. – Type from Malaysia, Sabah, Tawau Prov., NW of road Lahad Datu-Sandakan crossing with Segama river.

Cross diagnosis. Among Borneo *Arinia* identified by the presence of a short columellar tooth in the tuba, close to, and usually just visible in the aperture.

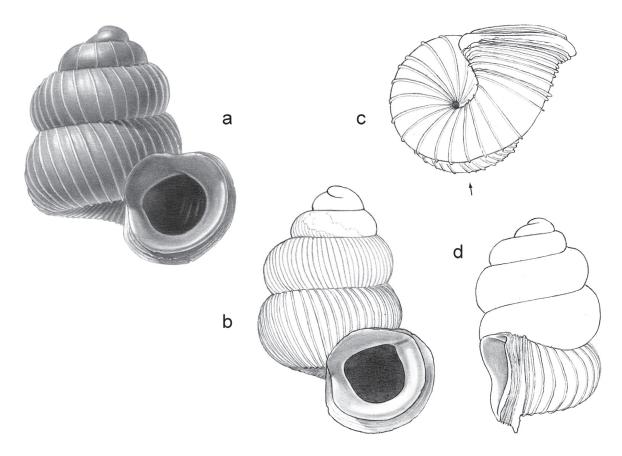


Fig. 42, a-d. *Arinia turgida* Vermeulen, 1996, a-b. Frontal view, shell 2.1 mm high, c. Umbilical view, arrow indicates constriction, d. Right lateral view.

Description. Shell approx. cylindrical, last two whorls widest. Whorls convex. Tuba with a short, longitudinal columellaris close to the aperture, and usually just visible. Sculpture. Radial ribs close to the apex single-crested, 10–20 ribs/0.5 mm, on the next whorls double-crested with both crests equally high, or with the distal crest highest, on the penultimate whorl 5–7 ribs/0.5 mm, absent above the aperture; ribs on the tuba single-crested again. Spiral striation absent. Aperture not turned upwards. Peristome: Palatal side not protruding beyond the penultimate whorl, columellar side not sinuous; outer peristome at most slightly spreading beyond the inner on the palatal and basal side, gradually narrowed on the columellar side, but more abruptly so towards the upper corner; inner peristome just above the upper corner with a (slight) protrusion about parallel to the margin, palatal side below this protrusion with a transverse furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height 1.25–1.70 mm; width 0.75–0.85 mm; ratio height/width 1.6–2.0; umbilicus closed but rimate in oblique view; number of whorls 4 1/8–5 1/8, including a tuba of 1/2–5/8 whorl; height and width aperture 0.30–0.35 mm.

Distribution in Sabah. Rare in E: Danum valley, Ulu Segama, Silam Coast Conservation Area. Elevation range: 0–300 m. In secondary woodland on sandy limestone bedrock. Endemic to Sabah.

Notes. The columellar tooth is reminiscent of *Diplommatina*.

Arinia streptaxiformis Vermeulen, 1996

(fig. 43g–k, map 6e)

Vermeulen 1996a: 114. – Type from Malaysia, Sabah, Tawau Prov., Segarong hills 25 km ESE of Kunak, Pababola hill.

Cross diagnosis. Identified among Borneo *Arinia* by the well-demarcated furrow in the tuba, on the columellar side, corresponding with a similar ridge on the outside.

Description. Shell approx. cylindrical, last two whorls widest. Whorls convex, last whorl sometimes moderately convex. Tuba with a rounded, well demarcated ridge on the columellar side (corresponding with a similar furrow inside); often with a short, longitudinal tooth in palatal, basal or almost columellar position, close to the

constriction. Sculpture. Radial ribs on the apical whorls single-crested, 5–11 ribs/0.5 mm, towards the penultimate whorl double-crested, usually with the distal crest highest, on the penultimate whorl 3–6 ribs/0.5 mm, above the aperture 4–5 ribs/0.5 mm, ribs close to the peristome often single-crested again. Spiral striation fine. Aperture not turned upwards, or sometimes slightly so, furrow in the tuba often just visible on the columellar side. Peristome: Palatal side usually distinctly protruding beyond the penultimate whorl, columellar side hardly to moderately sinuous; outer peristome hardly to moderately spreading beyond the inner on the palatal and basal side, abruptly narrowed on the columellar side and towards the upper corner; inner peristome just above the upper corner with a protrusion about parallel to the margin, palatal side below this protrusion with a distinct transverse furrow, palatal and basal side without a lip parallel to the margin. Dimensions. Height (1.5–)1.6–2.1 mm; width (0.9–)1 –1.4 mm; ratio height/width 1.3–1.8; umbilicus 0.25–0.65 mm wide; number of whorls (4 3/8–)5–5 5/8, including a tuba of (1/2–)3/4–1 1/4 whorl; height aperture 0.45–0.50 mm; width 0.4–0.5 mm.

Distribution in Sabah. Rare in E: Batu Tengar, Tun Sakaran Marine Park. Elevation range: 0–100 m. In primary forest and shrubby coastal vegetation, on limestone and volcanic bedrock. Endemic to Sabah.

Variability. Some specimens from Batu Tengar have the tuba partly detached from the spire.

Genus *Diplommatina* Benson, 1849

Diagnosis for the Sabah species. Shell white to orange to red(-brown). Tuba coiled around an axis which runs approx. parallel to the axis of the spire. Tuba with a columellar lamella (indistinct in some species) which in most species ends as a columellar tooth in the aperture. Aperture tilted downwards up to 30° relative to the coiling axis of the spire. Spire $(4 \frac{1}{2})5-8 \frac{1}{2}(-10)$ whorls, including a tuba of $3/4-1 \frac{3}{4}(-3)$ whorls.

KEY TO THE GROUPS

1 – Shell dextral

2 – Umbilicus open Group 1

2 – Umbilicus closed

3 – Either tuba 1 1/4–3 whorls long, or widest whorl without radial ribs, or both characters present

Group 2

3 – Tuba 3/4–1 1/8 whorl long. Radial ribs present on the widest whorl

4 – Columellar tooth in the aperture distinct when the shell is observed frontally

5 – Radial ribs distinctly sinuous

Group 5

5 – Radial ribs approx. straight

6 – Peristome double

Group 3 Group 4

6 – Peristome simple (because outer and inner peristome fused)

4 - Columellar tooth in the aperture not visible, or inconspicuous when the shell is observed frontally

7 – Constriction with a parietalis

Group 6 Group 7

7 – Constriction without a parietalis

1 – Shell sinistral

8 – Shell 1.3–1.5 mm high

Group 8

8 – Shell 4.3–10.3 mm high

9 – Peristome on the parietal side spreading up to the suture of the penultimate whorl

Group 9

9 - Peristome on the parietal side spreading but not reaching the suture of the penultimate whorl

10 – Constriction with 1–2 palatales

Group 10

10 – Constriction without palatalis

Group 11

Group 1

Diplommatina bidentata Vermeulen, Liew & Schilthuizen, 2015

(fig. 44a–b, map 8a)

Vermeulen et al. 2015: 31. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong c. 50 km WSW of Lahad Datu.

Cross diagnosis. Uniquely identified within *Diplommatina* by the parietal lamella, which runs along the full length of the tuba and which is visible as a parietal tooth deep in the aperture.

Description. Shell dextral, conical, with the last whorl or the last two whorls widest; sides of spire flat or slightly convex. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, with 1 parietalis which continues as a lamella down to the aperture, 1 longitudinal palatalis slightly to the left of the parietal peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture.

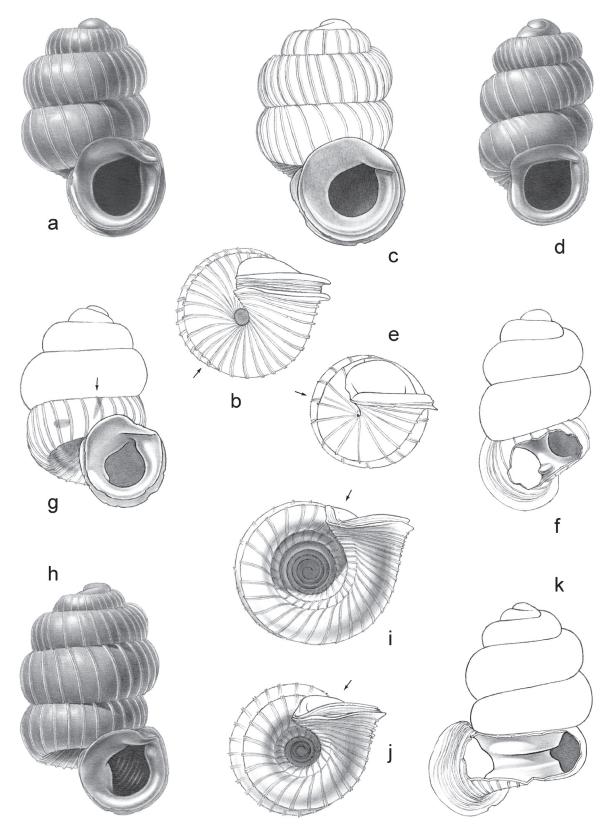


Fig. 43, a–b. *Arinia brevispira brevispira* Vermeulen, 1996, a. Frontal view, shell 1.9 mm high, b. Umbilical view, arrow indicates constriction; c. *Arinia brevispira orientalis* Vermeulen, 1996, frontal view, shell 2.0 mm high; d–f. *Arinia dentifera* Vermeulen, 1996, d. Frontal view, shell 2.1 mm high, e. Umbilical view, arrow indicates constriction, f. back view with part of the shell removed to show interior of the tuba; g–k. *Arinia streptaxiformis* Vermeulen, 1996, g. Frontal view, shell 1.8 mm high, h. Frontal view, shell 2.0 mm high, i–j. Umbilical views, arrows indicates constriction, k. back view with part of the shell removed to show interior of the tuba.

Radial ribs straight, distinct, rather low, rather wide, rather densely placed (7–11 ribs/0.5 mm on the penultimate whorl). Spiral striation present, inconspicuous, fine and dense. Aperture hardly tilted relative to the coiling axis of the spire; columellaris large, slightly downwards directed; the distal end of the parietalis visible on the parietal side as a tooth. Peristome double, expanded; palatal side only slightly sinuous, without edge; basal side without edge; basal corner not sinuous; outer peristome slightly spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, spreading on the parietal side. Dimensions. Height 1.90–2.30 mm; width 1.00–1.25 mm; ratio height/width 1.8–1.9; umbilicus 0.05–0.20 mm wide; number of whorls 6–6 3/4, including of a tuba of 7/8 whorl; height and width aperture 0.25–0.30 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 200–300 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Diplommatina toretos Vermeulen, 1993

(fig. 44c–f, map 8a)

Vermeulen 1993: 19; Marzuki et al. 2021: 26. – Type from Malaysia, Sarawak, 1st Div., mount Pangga 3 km ENE of Bau.

Description. Shell dextral, conical, last two whorls widest; sides of spire concave. Whorls convex. Suture impressed. Constriction about level with the edge between the parietal and the columellar side of the peristome, with 1 parietalis, usually 1 longitudinal palatalis, 1 transversal palatalis, 1 columellaris which continues as a lamella in the tuba. Sculpture. Radial ribs usually sinuous, distinct, rather high, rather wide, rather widely spaced to rather densely placed (2–5 ribs/0.5 mm on the penultimate whorl). Spiral striation present. Aperture hardly tilted relative to the coiling axis of the spire; columellaris usually not visible. Peristome double, expanding; palatal side not to slightly sinuous, with a moderate edge; basal side with or without a slight edge; basal corner sinuous, rather sharp; outer peristome usually spreading beyond the inner; inner peristome convex but usually without lip on the palatal side, expanding, free and sinuous on the columellar side, little spreading on the parietal side. Dimensions. Height 2.4–3.3 mm; width 1.2–1.4 mm; ratio height/width 1.8–2.5; umbilicus up to 0.1 mm wide; number of whorls 6 1/8–7 1/2, including a tuba of 3/4 whorl; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Highlands: Crocker range only. Elevation range: 1100–1200 m. In primary and secondary forest on sandstone/shale bedrock; elsewhere on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Notes. Diplommatina toretos strongly resembles D. soror or, in Sarawak, D. concinna H Adams, 1872 apart from the open umbilicus. The possibility that D. toretos consists of parasite-infected specimens of other Diplommatina species should be investigated.

Group 2

Diplommatina calvula Vermeulen, 1993

(fig. 45g-i, map 8a)

Vermeulen 1993: 26; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Sandakan Prov., 'North Borneo': Presumably (because found in an old sample of *D. sykesi*, which for a long time was only known from this locality) Kinabatangan river valley, Gomantong hill.

Description. Shell dextral, fusiform, penultimate whorl widest and bulging to the right in frontal view; sides of spire slightly concave. Whorls convex. Suture impressed. Constriction up to 3/4 whorl beyond the upper corner of the peristome, up the spire, with (only observed through the shell wall) 1 (?) parietalis, 1 longitudinal palatalis entirely beyond the upper corner of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs absent. Spiral striation absent. Aperture tilted up to 25° relative to the coiling axis of the spire; columellaris distinct, slightly directed downwards. Peristome double, expanding; palatal side somewhat sinuous, with or without a slight edge; basal side without edge; basal corner not sinuous, slightly protruding; outer peristome hardly to moderately spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, moderately spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.7–3.6 mm; width 1.1–1.6 mm; ratio height/width 2.2–2.6; number of whorls 7 1/4–8, including a tuba of 1 3/8–1 3/4 whorl; height aperture 0.5–0.8 mm; width aperture 0.5–0.7 mm.

Distribution in Sabah. Rare: Sapulut, lower Kinabatangan. Elevation range: 0–600 m. In (damp) primary forest over limestone bedrock. Endemic to Sabah.

Diplommatina madaiensis Vermeulen, 1993

(fig. 45d–f, map 8b)

Vermeulen 1993: 24. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Madai hill, 40 km SSW of Lahad Datu.

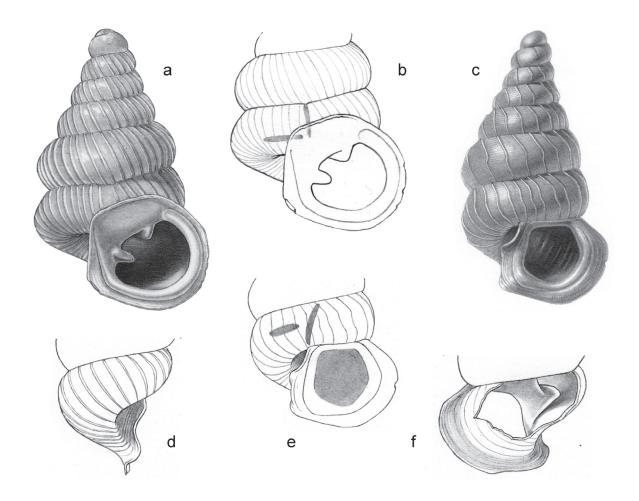


Fig. 44, a–b. *Diplommatina bidentata* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 2.3 mm high, b. Frontal view, with internal teeth indicated; c–f. *Diplommatina toretos* Vermeulen, 1993, c. Frontal view, shell 2.5 mm high, d. Frontal view, with internal teeth indicated, e. Left lateral view, f. Back view, part of the shell removed to show internal structure.

Cross diagnosis. Characterized within Group 2 (and among Borneo *Diplommatina*) by the tuba of 2–3 whorls long, versus 1–1 3/4 whorl. Also, it has radial ribs over the entire shell.

Description. Shell dextral, fusiform, lowermost but two whorls widest; penultimate whorl bulging to the right in frontal view; sides of spire concave. Whorls convex. Suture impressed. Constriction 1–2 whorls beyond the upper corner of the peristome, up the spire, with (only observed through shell wall) 1 (?) parietalis, 1 longitudinal palatalis entirely beyond the upper corner of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs over the entire shell, straight, rather distinct, low, rather wide, rather spaced (3–5 ribs/0.5 mm on the penultimate whorl). Spiral striation inconspicuous, on the top whorls only. Aperture tilted up to 25° relative to the coiling axis of the spire; columellaris distinct, not directed downwards. Peristome double, expanding; palatal side somewhat sinuous, without edge; basal side without edge; basal corner hardly sinuous, slightly protruding; outer peristome not spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, moderately spreading on the parietal side. Umbilicus closed. Dimensions. Height 3.1–3.7 mm; width 1.3–1.5 mm; ratio height/width 2.4–2.7; number of whorls 8 1/4–10, including a tuba of 2–3 whorls; height aperture 0.5–0.7 mm, width 0.5–0.6 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 100–200 m. In disturbed primary forest on limestone bedrock. Endemic to Sabah.

Diplommatina oedogaster Vermeulen, 1993

(fig. 45a-c, map 8b)

Vermeulen 1993: 27; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Interior Prov., Pun Batu approximately 30 km W of Sapulut.

Cross diagnosis. Resembles *Diplommatina calvula* and *D. sykesi*, other species of Group 2 partly or entirely without radial ribs, but differs by the shorter tuba (1 whorl, versus 1 1/4–1 3/4 whorl).

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire concave. Whorls: Apical whorls convex, next whorls almost flat, body whorl convex. Suture slightly impressed, well impressed at the body whorl. Constriction about level with the parietal side or with the upper corner of the peristome, with 1 parietalis, 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs absent. Spiral striation absent. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner hardly sinuous, rather sharp; outer peristome spreading beyond the inner; inner peristome with a lip on the palatal side, free and slightly erect on the columellar side, moderately spreading on the parietal side. Umbilicus closed. Dimensions. Height 3.0–3.5 mm; width 1.3–1.7 mm; ratio height/width 2.0–2.4; number of whorls 7 1/4–7 7/8, including a tuba of 7/8–1 whorl; height aperture 0.6–0.8 mm; width 0.6–0.7 mm.

Distribution in Sabah. Widespread but rare: Pun Batu, Sapulut, lower Kinabatangan, Tabin. Elevation range: 0–600 m. In primary forest and shrubland, also in secondary forest, all localities on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Similar species elsewhere. Diplommatina niahensis Godwin-Austen, 1889 (Sarawak) has a sinuous palatal side of the peristome.

Diplommatina sykesi Fulton, 1901

(fig. 45j-k, 50a, map 8c)

Fulton 1901: 244; Laidlaw 1950: 219; Vermeulen 1993: 25; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2003b: 42; Clements et al. 2008: 2762. – *Diplommatina (Sinica) sykesi* (Fulton) Kobelt 1902: 475; Von Martens 1908: 258; Zilch 1953a: 37. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Differs from *Diplommatina oedogaster* and *D. calvula* by the presence of radial ribs on the apical whorls.

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat to slightly concave. Whorls convex. Suture impressed. Constriction 1/4–1/2 whorl beyond the upper corner of the peristome, up the spire, with (only observed through shell wall) 1 parietalis, 1 longitudinal palatalis entirely beyond the upper corner of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs on the top whorls only, straight, inconspicuous to rather distinct, low, rather wide, rather densely placed near the apex, rather widely spaced on the next whorls. Spiral striation absent or inconspicuous, on the top whorls only. Aperture tilted up to 25° relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, expanding; palatal side not or hardly sinuous, without edge; basal side without edge; basal corner not or hardly sinuous, acute or protruding; outer peristome hardly to moderately spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, moderately spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.8–3.2 mm; width 1.1–1.4 mm; ratio height/width 2.0–2.5; number of whorls 7 1/8–8 1/4, including a tuba of 1 1/4–1 3/4 whorl; height aperture 0.5–0.7 mm; width aperture 0.5–0.6 mm.

Distribution in Sabah. Rare in E: lower Kinabatangan, Tabin, Danum valley. Elevation range: 0–200 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Group 3

Check also:

Diplommatina amblyrhombos (Group 4) may key out here; it differs from the species in Group 3 by its larger shell (shell height 3.5–3.7 mm, versus 1.7–3.1 mm).

Diplommatina baliana (Group 6). Specimens with a slight columellar tooth may key out here. In this group, it most resembles *D. cacuminulus*, particularly with respect to the tuba length; it differs by the less conspicuous columellar tooth in the aperture and the wider shell (shell width 1.3–1.4 mm, versus 0.8–1.1 mm).

Diplommatina cacuminulus Vermeulen, 1993

(fig. 46a–c, map 8c)

Vermeulen 1993: 33. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong, 50 km WSW of Lahad Datu.

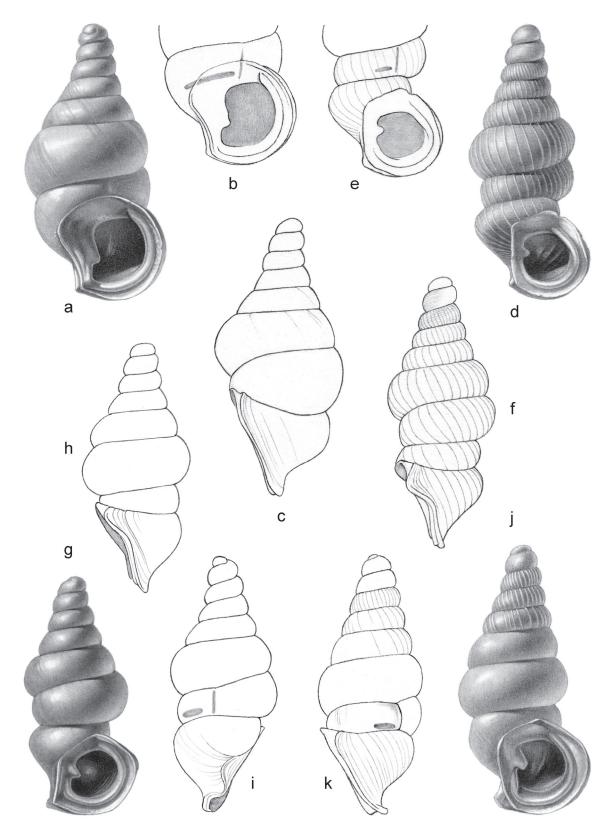


Fig. 45, a–c. *Diplommatina oedogaster* Vermeulen, 1993, a. Frontal view, shell 3.3 mm high, b. Frontal view, with internal teeth indicated, c. Right lateral view; d–f. *Diplommatina madaiensis* Vermeulen, 1993, d. Frontal view, shell 3.0 mm high, e. Frontal view, with internal teeth indicated, f. Right lateral view; g–i. *Diplommatina calvula* Vermeulen, 1993, g. Frontal view, shell 2.6 mm high, h. Right lateral view, i. Left lateral view, with internal teeth indicated; j–k. *Diplommatina sykesi* Fulton, 1901, j. Frontal view, shell 3.0 mm high, k. Right lateral view, with internal teeth indicated.

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat or slightly concave. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, sometimes close to the upper corner, with 1 parietalis, 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, rather distinct, rather low, rather wide, densely placed (7–10 ribs/0.5 mm on the penultimate whorl). Spiral striation present. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, expanding; palatal side not or hardly sinuous, with or without a slight edge; basal side without edge; basal corner not or hardly sinuous; outer peristome somewhat spreading beyond the inner; inner peristome with or without a lip on the palatal side, free and slightly erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.8–2.3 mm; width 0.8–1.1 mm; ratio height/width 2.0–2.5; number of whorls 6 5/8–7 1/2, including a tuba of 7/8–1 whorl; height and width aperture 0.3–0.4 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 100–300 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Diplommatina nevilli Crosse, 1870 (Peninsular Malaysia), has a sinuous basal corner of the peristome.

Diplommatina recta E A Smith, 1895

(fig. 46d–f, map 8c)

Smith 1895: 122; Kobelt & Von Möllendorff 1898: 137; Kobelt 1902: 442; Von Martens 1908: 258; Laidlaw 1950: 221; Vermeulen 1993: 33; 1996b: 284; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 64. – Type from Malaysia, Sabah, 'Kina Balu'.

Cross diagnosis. Characterized within Group 3 by the columellaris in the aperture, which continues to the edge of the inner peristome and there ends with a small knob.

Description. Shell dextral, approx. conical, last whorl moved inwards but still widest, sides of spire flat. Whorls convex. Suture impressed. Constriction level with the edge between the parietal and columellar side of the peristome, with (?) 1 parietalis (observed through the shell wall only), 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, rather distinct, rather low, rather thin, densely placed (6–9 ribs/0.5 mm on the penultimate whorl). Spiral striation fine, inconspicuous. Aperture slightly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards, continuing up to the edge of the inner peristome, there ending with a small knob. Peristome double, expanding; palatal side not or hardly sinuous, without edge; basal side without edge; basal corner not sinuous, rounded; outer peristome (hardly) spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.7–3.1 mm; width 1.3–1.5 mm; ratio height/width 1.8–2.3; number of whorls 6 1/8–6 3/4, including a tuba of 3/4 whorl; height and width aperture 0.6–0.7 mm.

Distribution in Sabah. Rare in W and N: Mount Kinabalu (old record), Balambangan, Malawali and Mengalum islands. Elevation range: 0–100 m, probably higher up on mount Kinabalu. Primary forest on sandstone/shale bedrock, dry primary coastal forest on limestone bedrock. Distribution elsewhere: Philippines (Balabac island only, just across the Sabah border).

Diplommatina strongyla Vermeulen, 1993

(fig. 46g-i, map 8d)

Vermeulen 1993: 29; Schilthuizen 2004: 94. – Type from Malaysia, Sarawak, 4th Div.: Gunung Subis (Batu Niah).

Cross diagnosis. Differs from *Diplommatina cacuminulus* by the palatal side of the peristome, which is distinctly sinuous (not or only slightly so in *D. cacuminulus*).

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat. Whorls convex. Suture impressed. Constriction level with the upper corner of the peristome or slightly beyond this point, up the spire, sometimes level with the parietal side of the peristome, with 1 parietalis, 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight (or slightly sinuous on the lowermost whorl), rather distinct, rather low, rather thin, densely placed (7–12 ribs/0.5 mm on the penultimate whorl). Spiral striation absent or inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire; columellaris rather distinct, directed downwards. Peristome double, moderately expanding; palatal side sinuous, with or without edge; basal side without edge; basal corner sinuous or not, almost acute; outer peristome hardly spreading beyond the inner; inner peristome with a lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.8–2.5 mm; width 1.0–1.2 mm; ratio height/width 1.6–2.1; number of whorls 5 1/8–6 3/8, including a tuba of approx. 1 whorl; height aperture 0.45–0.60 mm; width 0.4–0.5 mm.

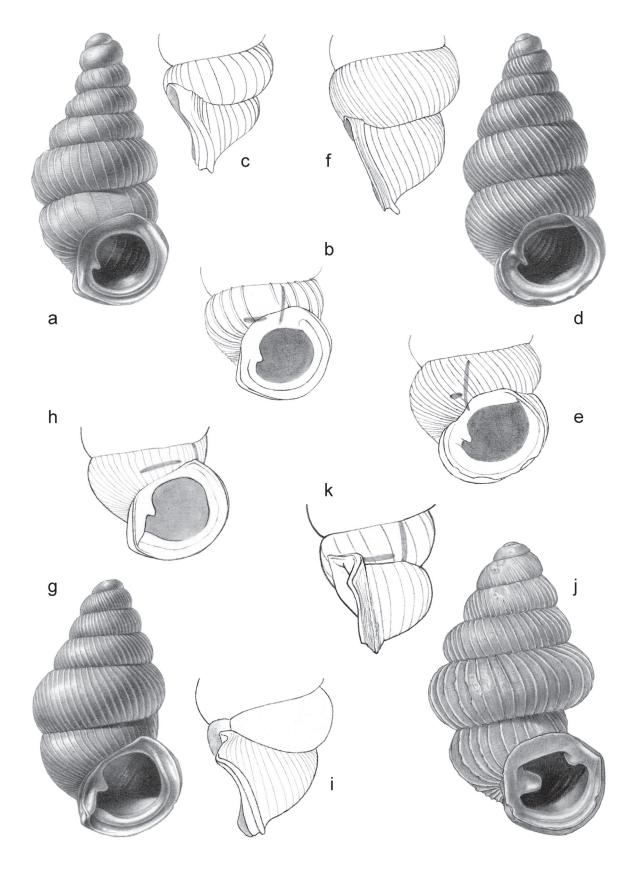


Fig. 46, a—c. *Diplommatina cacuminulus* Vermeulen, 1993, a. Frontal view, shell 2.0 mm high, b. Frontal view, with internal teeth indicated, c. Right lateral view; d—f. *Diplommatina recta* E A Smith, 1895, d. Frontal view, shell 2.8 mm high, e. Frontal view, with internal teeth indicated, f. Right lateral view; g—i. *Diplommatina strongyla* Vermeulen, 1993, g. Frontal view, shell 2.0 mm high, h. Frontal view, with internal teeth indicated, i. Right lateral view; j—k. *Diplommatina tylocheilos* Vermeulen, Liew & Schilthuizen, 2015, j. Frontal view, shell 1.8 mm high, k. Right lateral view.

Distribution in Sabah. Highlands: Crocker range only. Elevation range: 1100–1200 m. Damp disturbed primary forest on sandstone/shale bedrock. Elsewhere on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Similar species elsewhere. Differs from Diplommatina baritensis E A Smith, 1893 and D. onyx Fulton, 1901 (both from Sarawak) by its smaller size and less projecting peristome.

Variability. Some specimens have a distinctly more elongated spire than the one depicted. The basal corner is distinctly sinuous in material from elsewhere, but not in Sabah shells.

Diplommatina tylocheilos Vermeulen, Liew & Schilthuizen, 2015

(fig. 46j-k, map 8d)

Vermeulen et al. 2015: 32. - Type from Malaysia, Sabah, Interior Prov., mount Trus Madi slopes, Gua Loloposon.

Cross diagnosis. Uniquely identified among Sabah *Diplommatina* species by the distinct, conical, obtuse tooth on the palatal peristome, close to the upper corner.

Description. Shell dextral, fusiform, with the penultimate whorl widest, sides of spire flat. Whorls convex. Suture impressed. Constriction level with the upper corner of the peristome, or up to 1/8 whorl beyond this point, up the spire, with 1 parietalis, 1 longitudinal palatalis, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, distinct, rather low, narrow, rather densely placed (6–9 ribs/0.5 mm on the penultimate whorl). Spiral striation present, rather distinct, moderately spaced. Aperture hardly tilted relative to the coiling axis of the spire; columellaris large, horizontal; a second conical, obtuse tooth present on the palatal side, just below the upper corner. Peristome double, expanding; palatal side sinuous, with or without a slight edge; basal side without edge; basal corner not sinuous; outer peristome somewhat spreading beyond the inner; inner peristome with a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.75–2.05 mm; width 0.95–1.15 mm; ratio height/width 1.7–1.9; number of whorls 6–6 1/4, including a tuba of 1–1 1/8 whorl; height aperture 0.30–0.40 mm; width aperture 0.35–0.45 mm.

Distribution in Sabah. Highlands: Trus Madi range only. Elevation range: 1000–1100 m. Wet montane forest near stream, on limestone bedrock. Endemic to Sabah.

Group 4

Diplommatina amblyrhombos Vermeulen & Liew, new species

(fig. 47a-e, map 8b)

Type from Malaysia, Sabah, Kinabalu N.P., near Kotal route (holotype BOR/MOL 14791).

Cross diagnosis. Differs from the *Diplommatina* species of Group 3 and Group 4 by its size (shell 3.5–3.7 mm long, versus shell 1.7–3.1 mm long), and by the projecting, rounded wing on the palatal peristome, towards the upper corner (versus palatal peristome slightly angular at most).

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire approx. straight. Whorls convex. Suture impressed. Constriction situated slightly beyond the upper corner of the aperture, up the spire towards the apex, with 1 transversal palatalis, and 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, rather distinct, low, thin, moderately spaced (2–4 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture slightly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome simple (because outer and inner peristome fused), or indistinctly double on the columellar side only, expanding; palatal side sinuous, with a projecting, rounded wing towards the upper corner with a slightly inwards and sometimes upwards turned front edge, with an obtuse edge or a second less distinct wing towards the basal side; basal corner sinuous, with a distinct edge or a small rounded wing with or without a slightly inwards turned front edge; peristome with a slight, poorly demarcated lip on the palatal side, moderately spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 3.5–3.7 mm; width c. 2 mm; ratio height/width 1.7–1.9; number of whorls 6 1/8–6 3/8, including a tuba of approx. 1 1/8 whorl; height aperture 0.8–0.9 mm; width 0.9–1.0 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2600–3000 m. In wet subalpine forest, on granodiorite bedrock. Endemic to Sabah.

Name derivation. From ἀμβλύς (Ancient Greek) = blunt, and ῥόμβος = a rhombus, a lozenge, referring to the outline of the aperture.

Diplommatina plecta Fulton, 1901

(fig. 47f-h, map 8d)

Fulton 1901: 244; Laidlaw 1950: 217; Vermeulen 1993: 34; 1996b: 284; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Diplommatina (Sinica) plecta* (Fulton) Kobelt 1902: 470; Von Martens 1908: 258; Zilch 1953a: 35. – Type from Malaysia, Sabah, 'Kina Balu'.

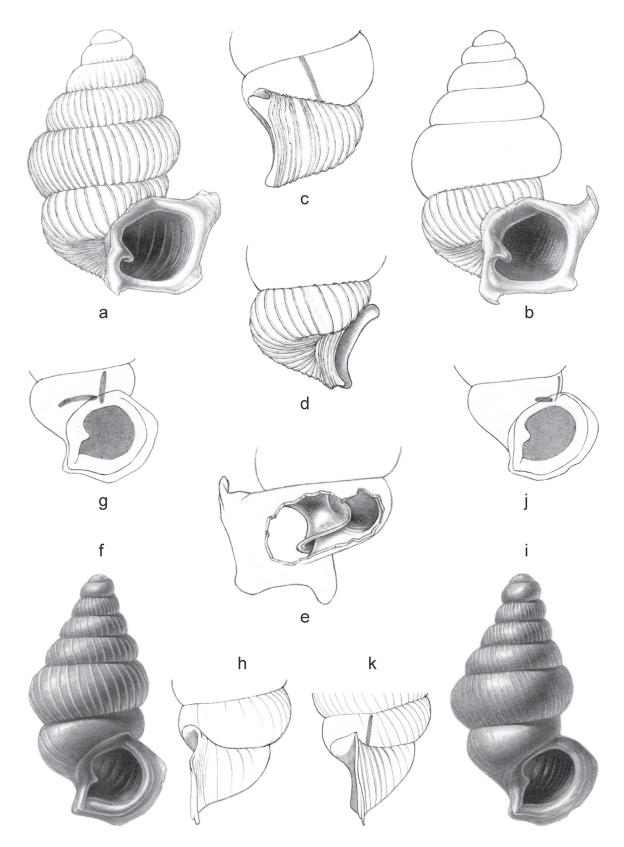


Fig. 47, a—e. *Diplommatina amblyrhombos* Vermeulen & Liew, new species, a. Frontal view, shell 3.6 mm high, b. Frontal view, from fragment, spire reconstructed, c. Right lateral view, with the position of the transverse palatal ridge in the constriction indicated, d. left lateral view, e. Back view, part of the shell removed to show internal structure; f—h. *Diplommatina plecta* Fulton, 1901, f. Frontal view, shell 2.7 mm high, g. Frontal view, with internal teeth indicated, h. Right lateral view; i—k. *Diplommatina tenuilabiata* Fulton, 1901, i. Frontal view, shell 2.7 mm high, j. Frontal view, with internal teeth indicated, k. Right lateral view.

Diplommatina baritensis auct. Smith 1895: 123; Laidlaw 1950: 216 (mount Kinabalu records only). Diplommatina welzeni auct. Liew et al. 2010: Online Supporting Information, Appendix 1. [Not Diplommatina baritensis E A Smith]. [Not Diplommatina welzeni Vermeulen].

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat or slightly concave. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, with 1 parietalis, 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, rather distinct, low, rather thin, rather densely placed, fading or absent towards the constriction and over (the first part of) the tuba (4–6 ribs/0.5 mm on the penultimate whorl). Spiral striation absent or fine, inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome simple (because outer and inner peristome fused), expanding; palatal side not or hardly sinuous, with an edge; basal side with an edge; basal corner moderately sinuous, slightly protruding; peristome with a lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.7–2.9 mm; width 1.3–1.6 mm; ratio height/width 1.8–2.1; number of whorls 6 5/8–6 7/8, including a tuba of 7/8 whorl; height aperture 0.5–0.7 mm; width 0.5–0.6 mm.

Distribution in Sabah. Rare in W: Kota Kinabalu, mount Kinabalu (old record), Crocker range, Trus Madi range. Elevation range: 100–800 m. In (disturbed) primary forest and secondary forest, on limestone and sand-stone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Diplommatina meratusensis Vermeulen, 1993 (Indonesia, Kalimantan) has a double peristome, as well as radial ribs not fading over the constriction.

Diplommatina tenuilabiata Fulton, 1901

(fig. 47i–k, map 8e)

Fulton 1901: 245; Laidlaw 1950: 217; Vermeulen 1993: 31. – *Diplommatina (Sinica) tenuilabiata* (Fulton) Kobelt 1902: 475; Von Martens 1908: 258; Zilch 1953a: 37. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

Diplommatina baritensis auct. Smith 1895: 123; Laidlaw 1950: 216 (Banggi island records only). [Not Diplommatina baritensis E A Smith].

Cross diagnosis. Tuba longer than in *Diplommatina plecta*, so that the constriction is right above the upper corner of the peristome or slightly beyond this point in the direction of the apex of the spire.

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire slightly concave. Whorls rather convex. Suture impressed. Constriction level with the upper corner of the peristome or slightly beyond this point, up the spire, with 1 parietalis, 1 longitudinal palatalis at the level of the peristome, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, rather inconspicuous, low, rather wide, rather densely placed, fading on the penultimate whorl (where 5–9 ribs/0.5 mm). Spiral striation absent or inconspicuous, on the top whorls only or over the entire shell. Aperture hardly tilted relative to the coiling axis of the spire; columellaris rather inconspicuous to rather distinct, not or hardly directed downwards. Peristome simple (because outer and inner peristome fused), expanding; palatal side not or hardly sinuous, with a slight edge; basal side usually with a slight edge; basal corner slightly to rather sinuous, sharp to slightly protruding; peristome with a slight to moderate lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.7–3.0 mm; width 1.3–1.5 mm; ratio height/width 1.9–2.2; number of whorls 6 3/4–7 1/8, including a tuba of 1 whorl; height aperture 0.7–0.8 mm; width 0.6–0.7 mm.

Distribution in Sabah. Rare in N: Banggi island, Kudat (old record), Sugut F.R. Elevation range: 0–100 m. In primary and secondary forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. The single specimen available from the Kudat area has a slightly thicker peristome, as well as an inconspicuous spiral striation over the entire shell.

Group 5

Diplommatina cyrtorhitis Vermeulen, 1993

(fig. 48a-c, map 8e)

Vermeulen 1993: 20; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1.
 Type from Malaysia, Sabah, Interior Prov., Pinangah river valley, Batu Urun (= Sinobang hill), from soil deposited at Tenom Agricultural Station.

Description. Shell dextral, about conical, last (two) whorls widest; sides of spire concave. Whorls convex. Suture impressed. Constriction about level with the edge between the parietal and columellar side of the peristome,

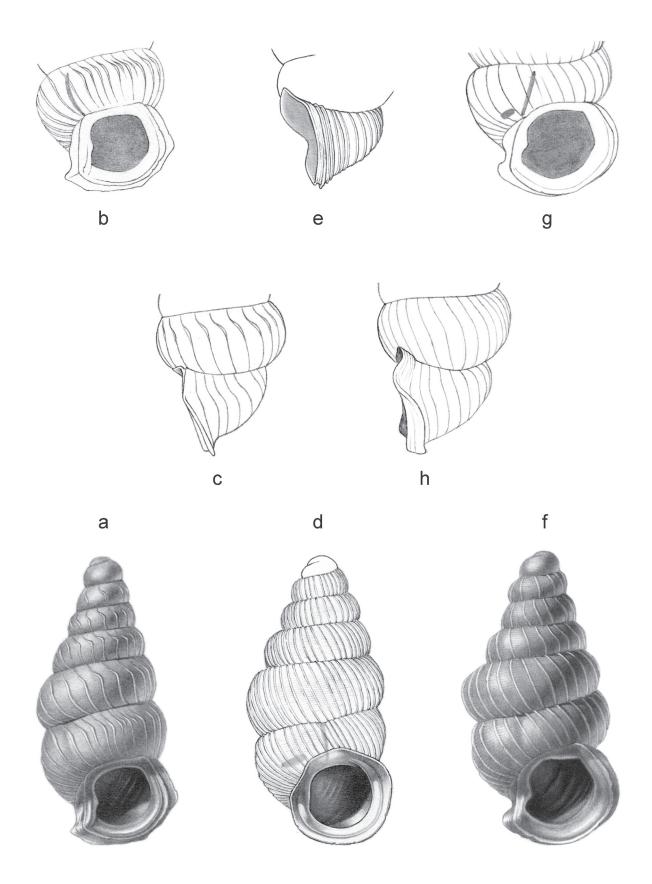


Fig. 48, a–c. *Diplommatina cyrtorhitis* Vermeulen, 1993, a. Frontal view, shell 2.5 mm high, b. Frontal view, with internal teeth indicated, c. Right lateral view; d–e. *Diplommatina baliana* Fulton, 1899, d. Frontal view, shell 2.8 mm high, e. Right lateral view; f–h. *Diplommatina soror* Vermeulen, 1993, f. Frontal view, shell 2.0 mm high, g. Frontal view, with internal teeth indicated, h. Right lateral view.

with 1 parietalis, 1 transversal palatalis, sometimes 1 longitudinal palatalis, 1 columellaris which continues as a lamella almost down to the aperture. Sculpture. Radial ribs distinctly sinuous, with a wide, well-rounded arc to the right, rather distinct, rather high, rather wide, rather densely placed (4–5 ribs/0.5 mm on the penultimate whorl). Spiral striation present, usually inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire; columellaris rather inconspicuous. Peristome double, expanding; palatal side not to slightly sinuous, with a slight edge; basal side with or without edge; basal corner hardly sinuous, protruding; outer peristome spreading beyond the inner; inner peristome with or without a lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.3–2.7 mm; width 1.1–1.3 mm; ratio height/width 1.8–2.3; number of whorls 6 3/8–7 3/8, including a tuba of 3/4 whorl; height aperture 0.4–0.6 mm; width aperture 0.4–0.6 mm.

Distribution in Sabah. Widespread; scattered localities in W; rare elsewhere: Meliau range, Tawau hills. Elevation range: 100–1600 m. In (disturbed) primary forest on limestone, sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Variability. A single shell with a longitudinal palatalis is recorded from Sapulut (Gua Pungiton).

Group 6

Check also:

Diplommatina cyrtorhitis (Group 5). Specimens with an inconspicuous columellaris are distinguished from species in Group 6 by the distinctly sinuous radial ribs.

Diplommatina baliana Fulton, 1899

(fig. 48d-e, map 8e)

Fulton 1899: 216; Nurinsiyah & Hausdorf 2017: 222. – *Diplommatina (Diplommatina) baliana* (Fulton) Kobelt 1902: 425; Rensch 1931: 386; Zilch 1953a: 19. – Type from Indonesia, Bali.

Diplommatina cyclostoma auct. Vermeulen & Whitten 1998: 47.

[Not Diplommatina cyclostoma Von Möllendorff].

Cross diagnosis. Diplommatina cacuminulus (Group 3) is rather similar but has a distinct columellar tooth in the aperture and has a slenderer shell (shell width 0.8–1.1 mm, versus 1.3–1.4 mm).

Description. Shell dextral, fusiform, penultimate whorl widest but not much wider than the last; sides of spire flat. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome or with the upper corner, with 1 parietalis, close to the columella, 1 longitudinal palatalis, 1 transversal palatalis; 1 columellaris which continues as a lamella in the tuba. Sculpture. Radial ribs straight, rather distinct, rather low and thin, densely placed (8–10 ribs/0.5 mm on the penultimate whorl). Spiral striation fine. Aperture hardly tilted relative to the coiling axis of the spire; columellaris just visible in most shells. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, rounded; outer peristome not or hardly spreading beyond the inner; inner peristome with a lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.3–3.1 mm; width 1.3–1.4 mm; ratio height/width 1.9–2.1; number of whorls 5 5/8–6 3/8, including a tuba of 3/4–7/8 whorl; height aperture 0.55–0.60 mm; width aperture 0.55–0.70 mm.

Distribution in Sabah. Ulu Segama only. Elevation: c. 100 m. Secondary vegetation on limestone bedrock. Distribution elsewhere: Indonesia (Java, Madura, Bali, Sumba).

Diplommatina soror Vermeulen, 1993

(fig. 48f-h, map 8f)

Vermeulen 1993: 22; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256, 257; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 94; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sarawak, 4th Div.: Beluru area SW of Marudi, near Vrong hill.

Cross diagnosis. Differs from *Diplommatina baliana* by the angular basal corner of the aperture (not rounded), and by the more widely spaced radial ribs (4–6 ribs/0.5 mm on the penultimate whorl, versus 8–10 ribs/0.5 mm).

Description. Shell fusiform, last (two) whorls widest; sides of spire concave. Whorls convex. Suture impressed. Constriction about level with the edge between the parietal and columellar side of the peristome, with 1 parietalis, with 1 longitudinal palatalis (may be absent in material from elsewhere), with 1 transversal palatalis, 1 columellaris which continues as a lamella almost down to the aperture. Sculpture. Radial ribs on the top whorls slightly sinuous, those on the widest whorl not or hardly so; rather distinct, rather high, rather wide, rather densely placed (4–6 ribs/0.5 mm on the penultimate whorl). Spiral striation present. Aperture hardly tilted relative to the coiling axis of the spire; columellaris inconspicuous. Peristome double, expanding; palatal side slightly to mod-

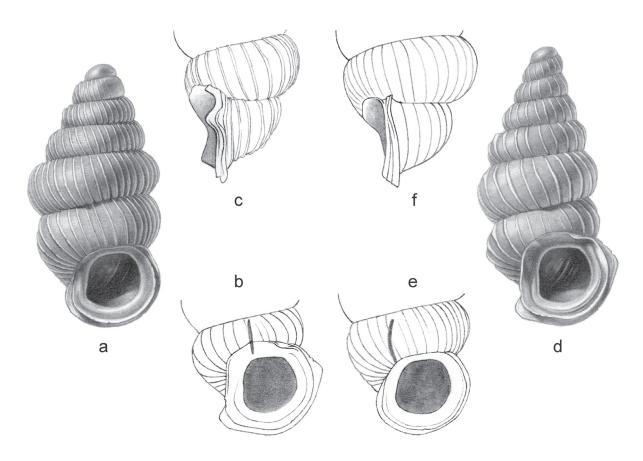


Fig. 49, a–c. *Diplommatina antheae* Vermeulen, 1993, a. Frontal view, shell 1.9 mm high, b. Frontal view, with internal teeth indicated, c. Right lateral view; d–f. *Diplommatina gomantongensis* E A Smith, 1894, d. Frontal view, shell 3.4 mm high, e. Frontal view, with internal teeth indicated, f. Right lateral view.

erately sinuous, with a slight edge; basal side with or without a slight edge; basal corner slightly sinuous, angular, protruding; outer peristome spreading beyond the inner; inner peristome with a lip on the palatal side, spreading over the shell, free on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.9–2.9 mm; width 0.9–1.4 mm; ratio height/width 2.0–2.4; number of whorls 5 7/8–7 3/8, including a tuba of 3/4 whorl; height aperture 0.4–0.7 mm; width aperture 0.4–0.6 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–1500 m. In (disturbed) wet or dry primary forest on sandstone/shale and limestone bedrock. Also in Sarawak. Endemic to Borneo.

Similar species elsewhere. Diplommatina concinna H Adams, 1872 (Sarawak) has a decollate shell, slightly sinuous radial ribs on the penultimate whorl, and a distinct columellaris in the aperture.

Variability. Sarawak specimens usually lack the longitudinal palatalis in the constriction.

Group 7

Diplommatina antheae Vermeulen, 1993

(fig. 49a-c, map 9a)

Vermeulen 1993: 17; Schilthuizen 2004: 94; Clements et al. 2008: 2761. – Type from Malaysia, Sabah, Interior Prov., Lian (Laying) Cave 12 km N of Keningau.

Diplommatina gomantongensis auct. Saul 1967: 109.

[Not *Diplommatina gomantongensis* E A Smith].

Cross diagnosis. Diplommatina gomantongensis is larger (shell height 2.5–3.5 mm versus 1.6–2.1 mm) and has more widely spaced radial ribs (3–5 ribs/0.5 mm on the penultimate whorl, versus 7–13 ribs/0.5 mm). Also, it usually has a slight edge along the palatal peristome (but see note below).

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, well away from the palatal side, with 1 transver-

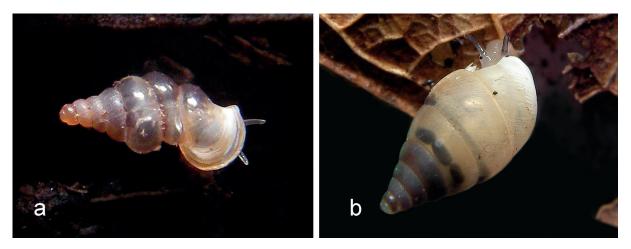


Fig. 50, a. Diplommatina sykesi Fulton, 1901; b. Diplommatina rubicunda (E Von Martens, 1867), juvenile specimen.

sal palatalis; a very inconspicuous columellaris is present half-way along the tuba. Sculpture. Radial ribs straight, rather distinct, rather low and thin, densely placed (7–13 ribs/0.5 mm on the penultimate whorl). Spiral striation inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire; columellaris not visible. Peristome double, expanding; palatal side not or hardly sinuous, usually without edge; basal side without edge; basal corner not sinuous, almost acute; outer peristome spreading beyond the inner; inner peristome with a slight lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.6–2.1 mm; width 0.8–1.0 mm; ratio height/width 1.8–2.2; number of whorls 5 3/4–6 5/8, including a tuba of 3/4–7/8 whorl; height and width aperture 0.3–0.4 mm.

Distribution in Sabah. Scattered localities in W. Elevation range: 300–1200 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Diplommatina maduana nefrens Vermeulen, 1993 (Sarawak) has a smaller number of whorls, as well as a wider spire. D. ventriculus Laidlaw, 1949 (Peninsular Malaysia and Indonesia, Sumatra) has a longitudinal palatalis.

Variability. Some shells of *Diplommatina antheae* from Batu Punggol also have a slight edge along the palatal peristome, like sympatric *D. gomantongensis*, but otherwise fit into *D. antheae*.

Diplommatina gomantongensis E A Smith, 1894

(fig. 49d–f, map 9b)

Smith 1894b: 464; Kobelt & Von Möllendorff 1898: 136; Kobelt 1902: 434; Von Martens 1908: 258; Laidlaw 1950: 215; Vermeulen 1993: 17; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – *Diplommatina symmetrica* Smith 1893b: 349. – Type from Malaysia, Sabah, 'Gomanton Hill'.

[Not Diplommatina symmetrica Hedley].

[Not Diplommatina gomantongensis auct. Saul 1967: 109; = Diplommatina antheae Vermeulen].

Description. Shell dextral, fusiform, penultimate whorl widest; sides of spire flat. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, well away from the palatal side, with 1 transversal palatalis; a very inconspicuous columellaris is present half-way along the tuba. Sculpture. Radial ribs straight, distinct, high, rather thin, rather widely spaced to rather densely placed (3–5 ribs/0.5 mm on the penultimate whorl). Spiral striation usually present. Aperture hardly tilted relative to the coiling axis of the spire; columellaris not or hardly visible if the shell is viewed frontally. Peristome double, expanding; palatal side moderately sinuous, with a moderate edge; basal side with or without a slight edge; basal corner not or slightly sinuous, narrowly rounded, often somewhat protruding; outer peristome spreading beyond the inner or not; inner peristome with a lip on the palatal side, usually free and slightly erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.5–3.5 mm; width 1.2–1.6 mm; ratio height/width 1.9–2.4; number of whorls 6 1/4–7 5/8, including a tuba of 3/4–7/8 whorl; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Rather common in S and E. Elevation range: 0–500 m. In wet or dry primary forest and shrub vegetation, in secondary forest, on limestone and sandstone/shale bedrock. Endemic to Sabah.

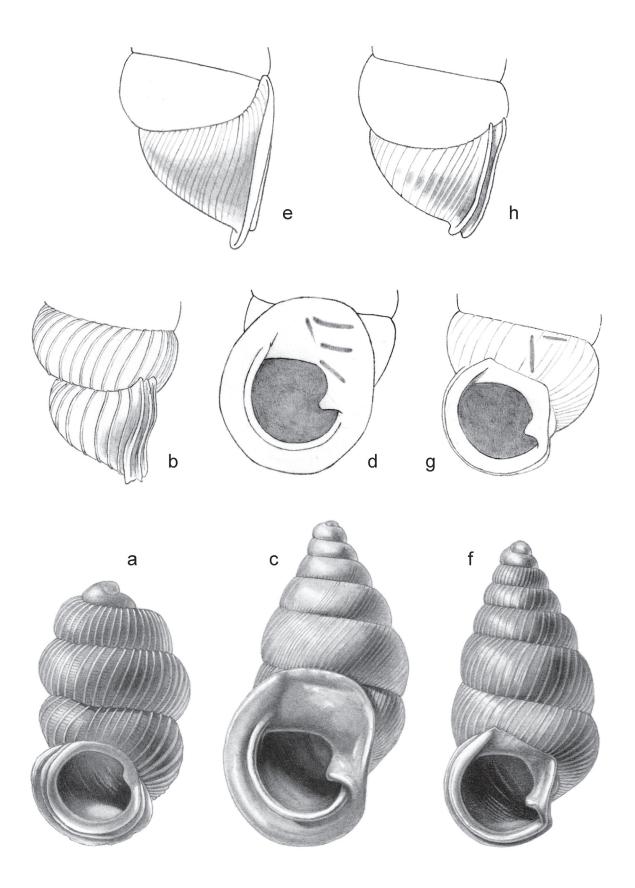


Fig. 51, a–b. *Diplommatina whiteheadi* E A Smith, 1898, a. Frontal view, shell 1.3 mm high, b. Left lateral view; c–e. *Diplommatina adversa* (H & A Adams, 1851), c. Frontal view, shell 5.8 mm high, d. Frontal view, with internal teeth indicated, e. Left lateral view; f–h. *Diplommatina centralis* Vermeulen, 1993, f. Frontal view, shell 4.5 mm high, g. Frontal view, with internal teeth indicated, h. Left lateral view.

Group 8

Diplommatina whiteheadi E A Smith, 1898

(fig. 51a-b, map 9c)

Smith 1898b: 34; Kobelt & Von Möllendorff 1898: 138; Kobelt 1902: 448; Von Martens 1908: 258; Vermeulen 1993: 34; 1996b: 285; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256, 257; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 94; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, 'Kina Balu'.

Description. Shell sinistral, about cylindrical, penultimate whorl widest; sides of spire convex. Whorls convex. Suture impressed. Constriction level with the parietal side of the peristome, with 1 parietalis, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs straight, distinct, rather high, rather thin, densely placed (9–12 ribs/0.5 mm on the penultimate whorl). Spiral striation distinct. Aperture slightly tilted relative to the coiling axis of the spire; columellaris rather distinct, not directed downwards. Peristome double or triple, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not or hardly sinuous, rounded or slightly angular; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, spreading over the shell on the columellar side, little spreading on the parietal side. Umbilicus closed. Dimensions. Height 1.3–1.5 mm; width 0.7–0.9 mm; ratio height/width 1.5–1.9, number of whorls 4 1/4–4 5/8, including a tuba of 3/4–7/8 whorl; height and width aperture 0.3–0.4 mm.

Distribution in Sabah. Widespread, scattered localities. Elevation range: 100–1700 m. In wet and dry primary forest, dry shrubland on limestone, sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Group 9

Diplommatina adversa (H & A Adams, 1851)

(fig. 51c–e, map 9d)

Godwin-Austen 1889: 348; Laidlaw 1950: 224; Vermeulen 1993: 36; Marzuki et al. 2021: 22. – *Paxillus adversus* H & A Adams 1851: 63; Pfeiffer 1855b: 185; 1858: 14; Von Martens 1867: 165; Issel 1874: 440; Kobelt & Von Möllendorff 1898: 142; Maassen 2001: 28. – *Gastroptychia adversa* (H & A Adams) Kobelt 1902: 481; Von Martens 1908: 258; Laidlaw 1949: 214. – Type from 'Singapore'.

Paxillus beccarii Issel 1874: 441; Pfeiffer 1876: 94. – Diplommatina beccarii (Issel) Godwin-Austen 1889: 348. – Gastroptychia beccarii (Issel) Von Martens 1908: 258. – Type from Malaysia, 'Sarawak'.

Diplommatina adversa (H & A Adams) var. natunensis Smith 1894b: 463. – Type from Indonesia, Natuna islands.

Description. Shell sinistral, fusiform, last two whorls widest; sides of spire slightly concave. Whorls slightly convex. Suture impressed. Constriction level with the parietal side of the peristome, with 1 parietalis, 3 longitudinal palatales, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs absent or inconspicuous, not sinuous, low, thin, densely placed (6–10 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome simple (because outer and inner peristome fused), palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, rounded; peristome with a lip on the palatal side, spreading but free and slightly erect on the columellar side, spreading up to the suture of the previous whorl on the parietal side. Umbilicus closed. Dimensions. Height 4.5–7.5 mm; width 2.1–3.3 mm; ratio height/width 2.0–2.3; number of whorls 6 1/8–7 3/8, including a tuba of 3/4–7/8 whorl; height aperture 1.3–1.8 mm; width 1.4–1.8 mm.

Distribution in Sabah. Ulu Segama only. Elevation range: 0–100 m. Secondary woodland on limestone bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Singapore, Indonesia (Natuna islands).

Notes. Probably introduced in Sabah. Elsewhere in Borneo, the species is restricted to W Sarawak and adjacent Kalimantan. The species could have moved to Sabah with planting material for the plantations surrounding the locality.

Group 10

Diplommatina centralis Vermeulen, 1993

(fig. 51f-h, map 9d)

Vermeulen 1993: 38; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 94; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Interior Prov., Batu Punggol SE of Sapulut.

Cross diagnosis. Within Group 10 identified by its small size (shell height 4.6–5.7 mm versus 6.0–8.1 mm), as well as by the well-spaced radial ribs (2–4 ribs/0.5 mm on the penultimate whorl, versus 5–10 ribs/0.5 mm). Shells

without a longitudinal palatalis resemble *Diplommatina subalpina* (Group 11); they differ by the coarser and more spaced radial sculpture (2–4 ribs/0.5 mm versus 7–12 ribs), and by the less convex whorls.

Description. Shell sinistral, fusiform to almost conical with the sides of the spire convex, last (two) whorls widest. Whorls all slightly convex. Suture slightly impressed. Constriction about level with the parietal side of the peristome or with the columellar corner, with or without 1 longitudinal palatalis parallel or oblique to the suture, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, rather inconspicuous, low, wide, (rather) widely spaced (2–4 ribs/0.5 mm on the penultimate whorl), often densely placed on the tuba. Spiral striation absent. Aperture slightly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner slightly sinuous, narrowly rounded; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 4.6–5.7 mm; width 2.2–2.8 mm; ratio height/width 1.8–2.3; number of whorls 6 3/4–7 3/8, including a tuba of 3/4–7/8 whorl; height aperture 1.1–1.3 mm; width 1.0–1.3 mm.

Distribution in Sabah. Widespread, rather common; not in N. Elevation range: 0–1500 m. In primary forest and secondary forest. Endemic to Sabah.

Similar species elsewhere. Diplommatina moluensis E A Smith, 1893 (Sarawak) has more prominent radial ribs, and two longitudinal palatales in the constriction.

Note. Shells from the Crocker range and mount Trus Madi all lack the longitudinal palatalis. See the diagnosis with the species of Group 10, where such shells of *D. centralis* would key out. Elsewhere, lack of a longitudinal palatalis occurs more occasionally.

Diplommatina electa Fulton, 1905

(fig. 52a–c, map 9e)

Laidlaw 1950: 226; Vermeulen 1993: 37; 1996b: 284; Schilthuizen 2004: 94. – *Diplommatina (Gastroptychia) electa* Fulton 1905: 94. – *Gastroptychia electa* (Fulton) Von Martens 1908: 258. – Type from Malaysia, 'N. Borneo'.

Description. Shell sinistral, fusiform to almost conical with the sides of the spire convex, last two whorls widest. Whorls all slightly convex. Suture slightly impressed. Constriction level with the parietal side of the peristome, close to the upper corner, with 1 parietalis, 1–2 longitudinal palatales, the upper (approx.) parallel to the suture, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, rather distinct, low, thin, densely placed (5–10 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, horizontal or directed downwards. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, narrowly rounded; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 6.0–7.0 mm; width 2.8–3.8 mm; ratio height/width 1.6–2.4; number of whorls 7 3/8–7 7/8, including a tuba of c. 3/4 whorl. Height aperture 1.4–1.9 mm; width 1.3–1.6 mm.

Distribution in Sabah. Highlands and surrounding lowlands in W: Mount Tambuyukon, mount Kinabalu, Crocker range. Elevation range: 100–3100 m. In primary and secondary forest, also found in a retaining wall along a roadside, on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Variability. The upper palatalis varies in length. Usually it is rather short (shorter than in *Diplommatina rubi-cunda*), but in some shells it is long, as, for instance, in the type specimen.

Diplommatina rubicunda (E Von Martens, 1864)

(fig. 50b, 52d–f, map 9e)

Godwin-Austen 1889: 348; Smith 1894b: 463; 1895: 122; Laidlaw 1950: 225; Vermeulen 1993: 37; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – Paxillus rubicundus Von Martens 1864a: 119; 1867: 164; Pfeiffer 1865: 13; Issel 1874: 440; Kobelt & Von Möllendorff 1898: 142. – Gastroptychia rubicunda (E Von Martens) Kobelt 1902: 483; Von Martens 1908: 258. – Type from Indonesia, W Kalimantan, 'Benkajang and Singkawang'.

Cross diagnosis. Among the species of Group 10 and Group 11 identified by the whorls just below the apex which are approx. flat, in contrast to the convex apical whorls and the slightly convex body whorls. All other species in the two groups have the whorls approx. equally convex from apex to constriction. It also differs from *Diplommatina electa*, the most similar species, by the much longer upper palatalis.

Description. Shell sinistral, fusiform to almost conical with the sides of the spire convex, close to the apex

slightly concave, last two whorls widest. Whorls: Top whorls convex, next whorls almost flat, body whorls slightly convex. Suture slightly impressed. Constriction level with the parietal side of the peristome or with the upper corner, with 1 parietalis, 1–2 longitudinal palatales, the upper parallel to the suture, the lower if present inconspicuous, approx. parallel to the suture, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, inconspicuous, low, wide, densely placed (5–9 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, horizontal or directed downwards. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, narrowly rounded; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 6.2–8.1 mm; width 3.0–4.0 mm; ratio height/width 1.9–2.3; number of whorls 6 7/8–8 1/8, including a tuba of 3/4–7/8 whorl; Height aperture 1.3–2.0 mm; width 1.2–2.0 mm.

Distribution in Sabah. Rather common in E; elsewhere Meliau range only. 0–200 m. Primary and secondary forest on limestone, sandstone/shale and serpentinite bedrock. Also in Sarawak. Endemic to Borneo.

Diplommatina rubra Godwin-Austen, 1889

(fig. 52g-i, map 9f)

Godwin-Austen 1889: 349; Laidlaw 1950: 225; Vermeulen 1993: 39; 1996b: 284; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Paxillus ruber* (Godwin-Austen) Kobelt & Von Möllendorff 1898: 142. – *Gastroptychia rubra* (Godwin-Austen) Kobelt 1902: 483; Von Martens 1908: 258; Laidlaw 1937: 188. – Type from Malaysia, Sarawak, 'Niah Hills'; possibly wrongly labeled because the species has not been found again there).

Diplommatina subisensis auct. Liew et al. 2010: Online Supporting Information, Appendix 1. [Not *Diplommatina subisensis* Vermeulen].

Cross diagnosis. Resembles Diplommatina electa, differs by the distinctly oblique upper longitudinal palatalis. Also, the last half-whorl is more distinctly convex: It bulges a little to the right if the shell is observed frontally. Shells of *D. centralis* with an oblique longitudinal palatalis are much smaller (shell height 4.6–5.7 mm versus 7.2–7.3 mm) and have more widely spaced radial ribs (2–4 ribs/0.5 mm on the penultimate whorl, versus c. 8 radial ribs).

Description. Shell sinistral, approx. conical with the sides of the spire convex, last whorl widest. Whorls all slightly convex, but last half-whorl moderately convex. Suture slightly impressed. Constriction level with the parietal side of the peristome, with (only observed through shell wall!) 1 parietalis, 1 short, oblique longitudinal palatalis, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, distinct, low, rather thin, densely placed (8 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture hardly tilted relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, somewhat narrowly rounded; outer peristome somewhat spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 7.2–7.3 mm; width 3.5–3.9 mm; ratio height/width 1.8–2.1; number of whorls c. 7 3/8, including a tuba of c. 7/8 whorl; height aperture 1.5–1.8 mm; width 1.7–1.9 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range. Elevation range: 1800–3200 m. In wet subalpine (Dacrydium-Leptospermum) forest, on granodiorite bedrock. Endemic to Sabah (but see note).

Note. The type of *Diplommatina rubra* was not available. Godwin-Austen's illustration of the type (1889: Plate 38, fig. 7), however, leaves little doubt about its identity. Its occurrence in Niah, Sarawak is doubtful, the species has not been found there again.

Group 11

Check also:

Diplommatina centralis and D. electa (Group 10). Resemble D. subalpina; see cross diagnosis with the latter.

Diplommatina megalotis Vermeulen & Liew, new species

(fig. 53a–c, map 9b)

Type from Malaysia, Sabah, Kinabalu N.P., near Kotal route (holotype BOR/MOL 14563). *Diplommatina* 'sp. 2' Liew et al. 2010: Online Supporting Information, Appendix 1.

Cross diagnosis. Uniquely identified among Borneo *Diplommatina* by its large size, in combination with the outer peristome which widens abruptly on the palatal side, at some distance from the upper corner, and narrows equally abruptly at the basal corner, and which spreads widely beyond the inner in between.

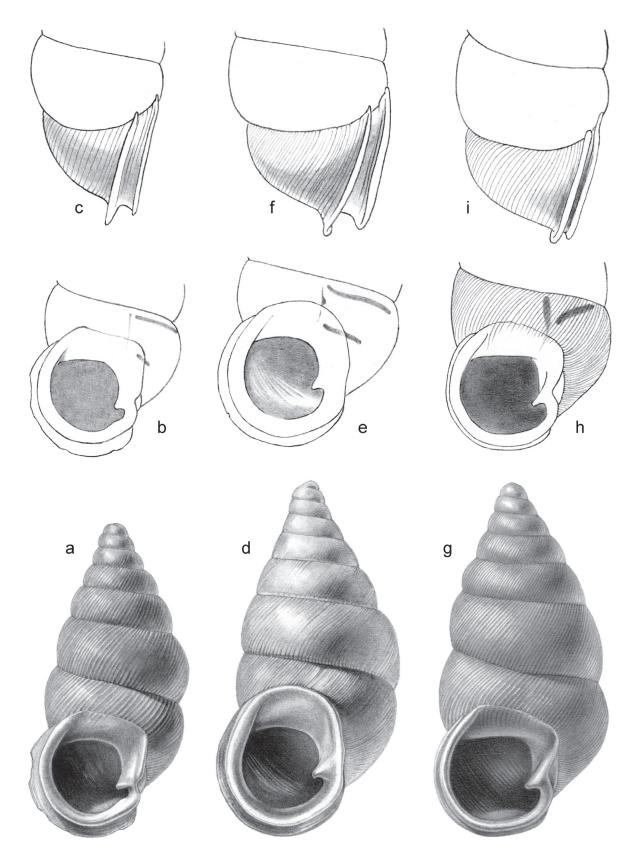


Fig. 52, a–c. *Diplommatina electa* Fulton, 1905, a. Frontal view, shell 6.5 mm high, b. Frontal view, with internal teeth indicated, c. Left lateral view; d–f. *Diplommatina rubicunda* (E Von Martens, 1864), d. Frontal view, shell 7.3 mm high, e. Frontal view, with internal teeth indicated, f. Left lateral view; g–i. *Diplommatina rubra* Godwin-Austen, 1889, g. Frontal view, shell 7.3 mm high, h. Frontal view, with internal teeth indicated, i. Left lateral view.

Description. Shell sinistral, ovoid-fusiform, with the last two whorls approx. equally wide; sides of spire slightly convex. Whorls moderately convex. Suture slightly impressed. Constriction level with the parietal side of the peristome (teeth not seen). Sculpture. Radial ribs not sinuous, fine, low, thin, rather widely spaced (3–4 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture tilted c. 20° relative to the coiling axis of the spire; columellaris large, slightly downwards directed. Peristome double, widely expanding; palatal and basal side not sinuous, evenly rounded; basal corner not sinuous, narrowly rounded; outer peristome abruptly widening on the palatal side, at some distance from the upper corner, and equally abruptly narrowing again at the basal corner, in between widely spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, widely spreading on the parietal side but not reaching the suture. Umbilicus closed. Dimensions. Height 8.0–10.0 mm; width 3.0–3.6 mm; ratio height/width 2.7–2.8, number of whorls 9–9 1/2, including a tuba of approx. 7/8 whorl; height aperture 1.8–2.2 mm and width aperture c. 2.0 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu. Elevation range: 1800–2300 m. In wet montane forest, on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Name derivation. From μέγας (Ancient Greek) = large, and $ο\mathring{\upsilon}\varsigma$ = ear.

Diplommatina subalpina Vermeulen & Liew, new species

(fig. 53g–i, map 10a)

Type specimens from Malaysia, Sabah, Kinabalu N.P., near Bowen route (holotype BOR/MOL 14578); ditto, near Kotal route (paratypes JV 14321/2 shells).

Diplommatina 'sp. 1' Liew et al. 2010: Online Supporting Information, Appendix 1.

Cross diagnosis. Differs from Diplommatina trusmadiensis by the small size (shell height 4.3–5.6 mm, versus 7.6–8.5 mm) and by the fusiform spire. In general shape and size it resembles shells of *D. centralis* (Group 10) without a longitudinal palatalis: It differs by the finer and denser radial sculpture (7–12 ribs/0.5 mm versus 2–4 ribs), and by the more convex whorls. It is also reminiscent of *D. electa* (Group 10), differs by the absence of a longitudinal parietalis and a longitudinal palatalis, and by its smaller size (shell height 4.3–5.6 mm versus 6.0–6.8 mm), and more convex whorls.

Description. Shell sinistral, fusiform with the last two whorls approx. equally wide, sides of spire convex. Whorls convex. Suture somewhat impressed. Constriction level with the parietal side of the peristome, close to the columellar corner, with 1 transverse palatalis, 1 inconspicuous columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, rather fine, low, rather thin, somewhat spaced (6–7 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture tilted c. 20° relative to the coiling axis of the spire; columellaris inconspicuous to rather distinct, directed downwards. Peristome double, expanding; palatal side slightly sinuous, without edge, basal side not sinuous, without edge; basal corner not sinuous, rounded; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 4.3–5.6 mm; width 2.6–3.3 mm; ratio height/width 1.6–2.0, number of whorls 5 1/2–6, including a tuba of c. 3/4 whorl; height aperture 1.2–1.5 mm; width 1.1–1.5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu. Elevation range: 2600–3500 m. In wet subalpine (Dacrydium-Leptospermum) forest, on granodiorite bedrock. Endemic to Sabah.

Name derivation. From the prefix sub- (Latin) = below, and alpinus = of the Alps, here: Of alpine environments.

Diplommatina trusmadiensis Vermeulen & Liew, new species

(fig. 53d–f, map 9f)

Type specimens from Malaysia, Sabah, mount Trus Madi, Gua Dawaras (holotype BOR/MOL 14837; paratypes JV 9871/2 shells).

Cross diagnosis. Differs from *Diplommatina subalpina* by the larger size (shell height 7.6–10.3 mm, versus 4.3–5.3 mm), and by the slenderer, almost conical spire.

Description. Shell sinistral, almost conical, with the last whorls slightly moved inwards but still widest, sides of spire approx. straight. Whorls moderately convex. Suture slightly impressed. Constriction level with the parietal side of the peristome, close to the columellar corner, with 1 transverse palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, fine, low, thin, densely placed (7–12 ribs/0.5 mm on the penultimate whorl). Spiral striation absent. Aperture tilted c. 20° relative to the coiling axis of the spire; columellaris small, directed downwards. Peristome double, expanding; palatal and basal side not sinuous, without edge; basal corner not sinuous, rounded; outer peristome spreading beyond the inner; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 7.6–10.3 mm; width 3.5–4.4 mm; ratio height/width 2.1–2.4, number of whorls 7

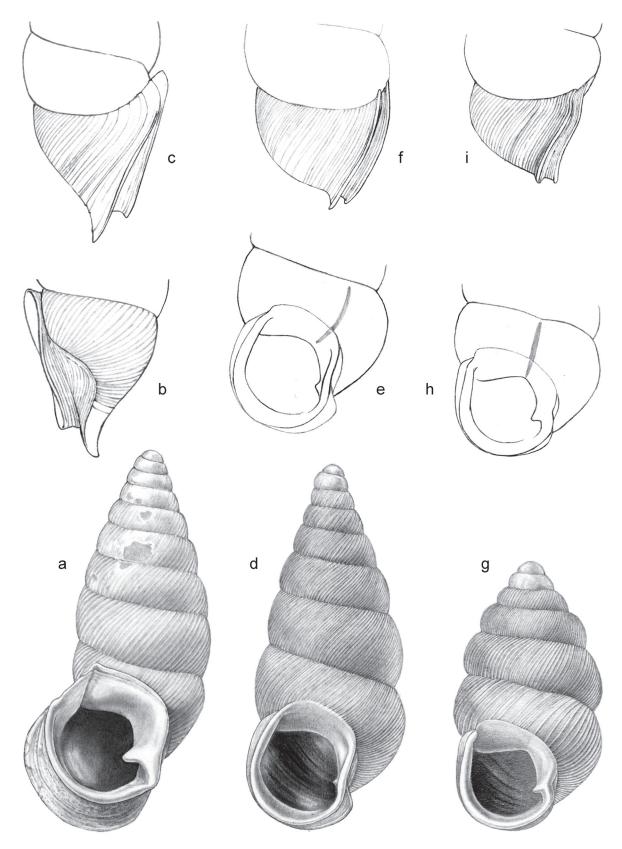


Fig. 53, a–c. *Diplommatina megalotis* Vermeulen & Liew, new species, a. Frontal view, shell 9.5 mm high, b. Right lateral view, c. Left lateral view; d–f. *Diplommatina trusmadiensis* Vermeulen & Liew, new species, d. Frontal view, shell 8 mm high, e. Frontal view, with internal teeth indicated, f. Left lateral view; g–i. *Diplommatina subalpina* Vermeulen & Liew, new species, g. Frontal view, shell 5.2 mm high, h. Frontal view, with internal teeth indicated, i. Left lateral view

5/8-8 1/2, including a tuba of 3/4-7/8 whorl; height aperture 1.8-2.2 mm and width aperture 1.8-2.2 mm.

Distribution in Sabah. Highlands: Mount Trus Madi only. Elevation range: 1400–1500 m. In wet montane forest, on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Resembles *Diplommatina sulphurea* E A Smith, 1893, from Sarawak, differs by the double peristome and the larger size (shell height 7.6–10.3 mm versus 5.9–6.6 mm).

Note. Fresh shells are lemon yellow with a purple apex.

Name derivation. Name referring to the type locality, mount Trus Madi.

Genus Moussonia O Semper, 1865

Diagnosis for the Sabah species. Shell white to red(-brown). Tuba coiled around an axis which runs approx. parallel to the axis of the spire. Tuba with a columellar lamella which ends as a columellar tooth in the aperture. Aperture tilted downwards $45-60^{\circ}$ relative to the coiling axis of the spire. Spire 6 7/8–8 1/4 whorls, including a tuba of 5/8-3/4 whorls.

Moussonia asynaimos (Vermeulen, 1993)

(fig. 54a–c, map 10b)

Diplommatina asynaimos Vermeulen 1993: 20; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2762.

– Type from Malaysia, Sarawak, 5th Div., Limbang river valley, 2 miles NE of the junction of Medalan river and Limbang river.

Description. Shell dextral, strictly conical, sides of spire slightly concave. Whorls: Top whorls convex, others obtusely angular at the periphery, almost flat above and below. Suture impressed. Constriction about level with the edge between the parietal and columellar side of the peristome, with 1 parietalis, 1 longitudinal palatalis, 2 columellares, the upper very prominent and with a low ridge which starts at its crest and runs over its lower surface towards its base, close to the aperture, the lower small and short. Sculpture. Radial ribs straight, rather distinct, low, rather wide, very densely placed (10–12 ribs/0.5 mm on the penultimate whorl). Spiral striation inconspicuous. Aperture tilted about 60° relative to the coiling axis of the spire; columellaris distinct, directed downwards. Peristome double, hardly expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, rounded; outer peristome hardly spreading at all; inner peristome without a lip on the palatal side, free and erect on the columellar side, somewhat spreading on the parietal side. Umbilicus closed. Dimensions. Height 2.2–2.8 mm; width 1.2–1.4 mm; ratio height/width 1.7–2.2; number of whorls 7 1/8–9 7/8, including a tuba of 5/8–3/4 whorl; height aperture 0.3–0.4 mm; width 0.5–0.6 mm.

Distribution in Sabah. Scattered localities in E; elsewhere Kuamut river only. Elevation range: 0–200 m, elsewhere up to 1200 m. In (disturbed) primary forest and shrubland, in secondary vegetation, on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Moussonia isseli (Godwin-Austen, 1889)

(fig. 54d–f, map 10b)

Diplommatina isseli Godwin-Austen 1889: 348; Vermeulen 1993: 35; Schilthuizen 2004: 94; Clements et al. 2008: 2762; Marzuki et al. 2021: 24. – Diplommatina (Pseudopalaina) isseli (Godwin-Austen) Kobelt & Von Möllendorff 1898: 139; Kobelt 1902: 453; Von Martens 1908: 258. – Type from Malaysia, Sarawak, 'Sarawak proper'.

Cross diagnosis. Differs from Moussonia asynaimos by the sinistral shell with rounded periphery.

Description. Shell sinistral, conical, sides of spire approx. straight. Whorls rounded. Suture impressed. Constriction level with the columellar side of the peristome, with 1 very short oblique palatalis close to the suture, 1 transversal palatalis, 1 columellaris which continues as a lamella down to the aperture. Sculpture. Radial ribs not sinuous, distinct, rather low, rather thin, densely placed (4–5 ribs/0.5 mm on the penultimate whorl). Spiral striation present or not. Aperture tilted about 45° relative to the coiling axis of the spire; columellaris distinct, not directed downwards. Peristome simple (because outer and inner peristome fused) or double, moderately expanding; palatal side not sinuous, without edge; basal side without edge; basal corner not sinuous, rounded; outer peristome hardly spreading beyond the inner; inner peristome without a lip on the palatal side, spreading but free on the columellar side, little spreading on the parietal side. Umbilicus open, narrow. Dimensions. Height 3.0–5.1 mm; width 1.7–2.5 mm; ratio height/width 1.7–2.1; number of whorls 6 1/8–8 1/4, including a tuba of 5/8 whorl; height aperture 0.4–0.8 mm; width aperture 0.8–1 mm.

Distribution in Sabah. Rare in W: Crocker range, Trus Madi range, Sinobang. Elevation range: 300–1900 m. In damp primary forest. Also in Sarawak. Endemic to Borneo.

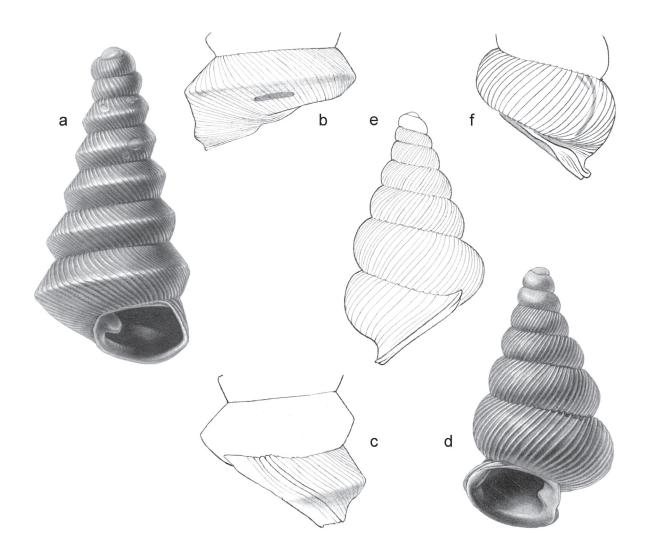


Fig. 54, a–c. *Moussonia asynaimos* (Vermeulen, 1993), a. Frontal view, shell 2.6 mm high, b. Back view, with internal teeth indicated, c. Right lateral view; d–f. *Moussonia isseli* (Godwin-Austen, 1889), d. Frontal view, shell 4.25 mm high, e Left lateral view, f. Right lateral view, with internal teeth indicated.

Genus *Opisthostoma* W T & H Blanford, 1860

Diagnosis for the Sabah species. Shell white. Tuba coiled around an axis at a distinct angle to the axis of the spire. Aperture tilted up to 90° relative to the coiling axis of the spire. Spire (excluding tuba) with 3–3 3/4 whorls.

KEY TO THE GROUPS

1 – Tuba distant from the spire

Group 1

- 1 -Tuba attached to the spire
 - 2 Aperture in frontal view with two teeth visible

Group 2

2 – Aperture in frontal view without visible teeth

Group 3

Group 1

Opisthostoma telestoma Vermeulen, 1991

(fig. 55a-c, map 10c)

Vermeulen 1991: 143; 1994: 90; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Interior Prov., Pun Batu approximately 30 km W of Sapulut.

Description. Spire ellipsoid-cylindrical, with the penultimate whorl widest if the shell is observed frontally. Apex moderately oblique, somewhat elevated. Whorls convex, rounded, last whorl moderately rounded towards the constriction. Constriction with 2 teeth: 1 distinct, oblique, short, high infra-columellaris, 1 inconspicuous, transverse, long, low palatalis. Tuba entirely distant from the spire, gradually narrowed towards the constriction, circular in section, rounded below. Sculpture. Radial ribs widely spaced near the apex, moderately spaced and low on the upper body whorl (3–5 ribs/0.5 mm), slightly more prominent and wider spaced on the lower body whorl, widely spaced, inconspicuous and low over the area of the constriction, and widely spaced, distinct and very high on the tuba. Spiral striation fine. Aperture tilted up to 30° relative to the coiling axis of the body whorls, with the upper margin at most level with the apex, widely ovate, teeth absent; inner peristome thickened, moderately spreading; outer peristome distinctly flaring on the palatal side. Dimensions. Height of spire without tuba 0.9–1.2 mm; width 0.8–1.0 mm; ratio height/width 1.1–1.2; umbilicus 0.15–.20 mm wide; number of whorls 3–3 3/4, excluding a tuba of approx. 1/2 whorl; height of aperture c. 0.5 mm; width of aperture 0.5–0.6 mm.

Distribution in Sabah. Widespread but rare: Banggi island, Pun Batu. Elevation range: 0–600 m. In shrubby woodland and coastal vegetation on limestone bedrock. Endemic to Sabah.

Group 2

Opisthostoma hailei Solem, 1964

(fig. 55d-e, map 10c)

Solem 1964: 18; Saul 1967: 110; Vermeulen 1991: 147; 1994: 94; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data. – Type from Malaysia, Sabah, Sandakan Prov., Gomantong Hill.

Description. Spire approx. cylindrical, with the last two whorls approx. equally wide if the shell is observed frontally. Apex somewhat oblique, moderately elevated. Whorls convex, rounded, the widest (narrowly) rounded at the periphery, last whorl moderately convex towards the constriction. Constriction with 2(–3) teeth: 1 parietalis projecting into the tuba, 1 distinct, oblique, short, rather high infra-columellaris; palatalis absent, sometimes present but very inconspicuous. Tuba attached to the spire, gradually narrowed towards the constriction, somewhat triangular in section, somewhat angular below. Sculpture. Radial ribs widely spaced near the apex, moderately spaced and low on the upper body whorl (6–9 ribs/0.5 mm), approximately similar but somewhat wider spaced on the lower body whorl and over the area of the constriction, and moderately spaced and slightly more prominent on the tuba. Spiral striation fine. Aperture tilted up to 15° relative to the coiling axis of the body whorls, with the upper margin at most approx. level with the apex, subtriangular, teeth 2: 1 very short, knob-like along the upper margin, close to the peristome; 1 long, lamella-like along the lower margin (the distal end of the parietalis in the constriction); inner peristome moderately thickened, moderately spreading; outer peristome distinctly flaring on the palatal side. Dimensions. Height of spire without tuba 1.0–1.3 mm; width 1.0–1.1 mm; ratio height/width 1.0–1.2; umbilicus 0.15–0.2 mm wide; number of whorls 3 1/8–3 1/2, excluding a tuba of approx. 1/2 whorl; height and width of aperture 0.4–0.7 mm.

Distribution in Sabah. Locally common in E: Lower Kinabatangan; elsewhere rare: Crocker range. Elevation range: 0–1900 m. In (disturbed) lowland forest and shrubby vegetation on limestone bedrock. Endemic to Sabah.

Group 3

Opisthostoma brachyacrum lambii (Vermeulen, 1991)

(fig. 56a-d, map 10d)

Vermeulen 1994: 98; Schilthuizen 2004: 94; Clements et al. 2008: 2762; Marzuki et al. 2021: 27. – *Opisthostoma lambii* Vermeulen 1991: 155; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, Interior Prov., Lian Cave 12 km N of Keningau.

Opisthostoma tarphypleura Vermeulen 1991: 153. – Type from Malaysia, Sarawak, 1st Div., W of Kampong Lobang Batu, 12.5 km S of Tebakang.

Cross diagnosis. Differs from *Opisthostoma javanicum* and *O. lechria* by the presence of a parietalis in the constriction. *Opisthostoma javanicum* from Sabah differs by the much wider ultimate whorl of the spire.

Description. Spire somewhat ellipsoid-cylindrical, with the penultimate whorl widest if the shell is observed frontally. Apex moderately to distinctly oblique, moderately elevated. Whorls convex, rounded, last whorl moderately rounded towards the constriction. Constriction with 3–4 teeth: 1 longitudinal, short, angularis (missing in some specimens); 1 longitudinal parietalis which is usually long and projects into the tuba; 1 distinct, oblique, rather high infra-columellaris; 1 distinct, transverse palatalis. Tuba attached to the spire, gradually narrowed towards the constriction, approx. circular in section, rounded below. Sculpture. Radial ribs very densely placed near

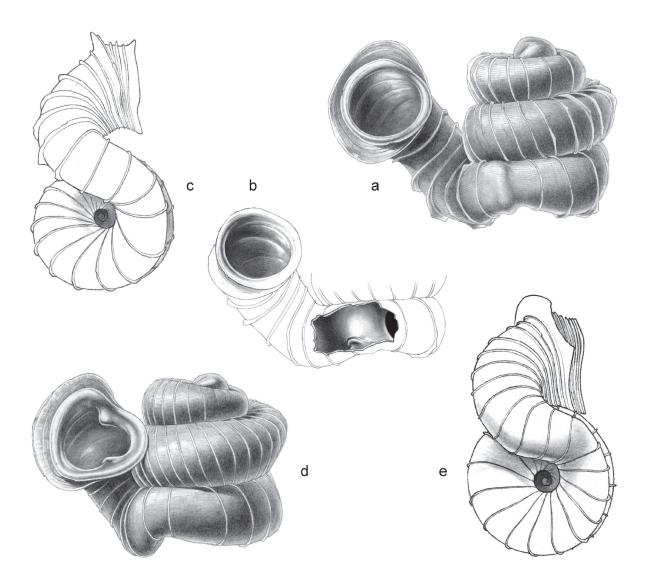


Fig. 55, a–c. *Opisthostoma telestoma* Vermeulen, 1991, a. Frontal view, shell 1.3 mm high, b. Frontal view, part of the shell removed to show tooth in the constriction, c. Umbilical view; d–e. *Opisthostoma hailei* Solem, 1964, d. Frontal view, shell 1.15 mm high, e. Umbilical view.

the apex, rather densely placed and rather low on the upper body whorl (10–13 ribs/0.5 mm), approximately similar but slightly wider spaced on the lower body whorl, again more widely spaced over the area of the constriction, and moderately spaced and slightly more prominent on the tuba. Spiral striation fine. Aperture tilted up to 30° relative to the coiling axis of the body whorls, with the upper margin at most level with the apex, widely ovate to circular, teeth absent; inner peristome moderately thickened, moderately spreading; outer peristome moderately flaring on the palatal side. Dimensions. Height of spire without tuba 0.8–0.9 mm; width 0.7–0.8 mm; ratio height/ width 1.1–1.2; umbilicus closed or open, up to 0.15 mm wide; number of whorls 3 1/8–3 5/8, excluding a tuba of approx. 1/2 whorl; height of aperture 0.4–0.5 mm; width of aperture 0.5–0.6 mm.

Distribution in Sabah. Scattered localities in W. Elevation range: 300–1600 m. In primary and secondary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Sabah specimens usually have a long parietalis, projecting deep into the tuba. However, some shells have a short parietalis, about as long as the angularis and not projecting in the tuba. In some such specimens the angularis may be absent.

Note. Opisthostoma brachyacrum is an unresolved species complex. Vermeulen (1994) distinguishes subspecies mainly on account of the configuration of the teeth in the constriction. Generally, subsp. lambii differs from subsp. brachyacrum by the presence of a short angularis in the constriction. Only in the limestone ranges S of

Kuching, Sarawak, where the two subspecies occur together, morphological intermediates are virtually absent. In populations elsewhere (of subsp. *brachyacrum* in E Sarawak and subsp. *lambii* in Sabah), intermediate specimens occasionally occur, often in specimens in which all teeth in the constriction are inconspicuous. Vermeulen (1994: 98) includes these intermediates in the subspecies with which they occur sympatrically. Pending further investigation, preferably including molecular phylogeny, we follow Vermeulen (1994), and we include in subsp. *lambii* some Sabah specimens which, based on characters, should be included in subsp. *brachyacrum*. Resolving this complex is beyond the scope of this work.

Opisthostoma javanicum Van Benthem Jutting, 1932

(fig. 56e–g, map 10d)

Van Benthem Jutting 1932: 203; 1948: 588; Vermeulen 1994: 101; Maassen 1997: 45; Vermeulen & Whitten 1998: 51; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Nurinsiyah & Hausdorff 2017: 239. – Type from Indonesia, Java, 'Tjampea near Buitenzorg'.

Opisthostoma aetheroscopa Vermeulen 1991: 155. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Description. Spire cylindrical, with the last two whorls approx. equally wide if the shell is observed frontally. Apex somewhat oblique, moderately elevated. Whorls convex, rounded, last whorl sometimes slightly angular, moderately rounded towards the constriction. Constriction with 2 teeth: 1 rather inconspicuous, slightly oblique, rather low infra-columellaris projecting over the lower palatal wall, at some distance and approximately parallel to the palatalis, 1 rather inconspicuous, transverse, long, low palatalis. Tuba attached to the spire, gradually narrowed towards the constriction, circular in section, rounded below. Sculpture. Radial ribs widely spaced near the apex, slightly more prominent and moderately spaced on the lower body whorl (8–11 ribs/0.5 mm), more widely spaced again over the area of the constriction, and widely spaced and rather high on the tuba. Spiral striation fine. Aperture tilted 60–90° relative to the coiling axis of the body whorls, with the upper margin at most level with the apex, widely ovate, teeth absent; inner peristome somewhat thickened, slightly spreading; outer peristome distinctly flaring on the palatal side. Dimensions. Height of spire without tuba 0.7–0.9 mm; width 0.8–0.9 mm; ratio height/ width 0.8–1.0; umbilicus c. 0.2 mm wide; number of whorls 3 1/8–3 1/2, excluding a tuba of approx. 1/2 whorl; height and width of aperture c. 0.5 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In disturbed primary forest. Elsewhere in a wide range of pristine and degraded vegetation types. On limestone bedrock. Also in Kalimantan. Distribution elsewhere: Indonesia (Java, Madura, Bali, Sulawesi).

Note. The description applies to Sabah material. The Sabah population differs from the type by the wide last whorl of the spire and by the wide umbilicus. In SE Kalimantan populations occur which are intermediate between the type and the Sabah shells.

Opisthostoma lechria Vermeulen, 1991

(fig. 56h, map 10e)

Vermeulen 1991: 157; 1994: 100. – Type from Malaysia, Sabah, Interior Prov., Pun Batu approximately 30 km W of Sapulut.

Cross diagnosis. Differs from Sabah *Opisthostoma javanicum* by the distinctly inwards-turned last whorl (before the start of the tuba).

Description. Spire obliquely ellipsoid, with the penultimate whorl widest and the last whorl distinctly narrower if the shell is observed frontally. Apex moderately oblique, moderately elevated. Whorls convex, rounded, last whorl moderately rounded towards the constriction. Constriction with 2 teeth: 1 distinct, slightly oblique, short, rather high infra-columellaris, 1 rather inconspicuous, transverse, long, low palatalis. Tuba attached to the spire, gradually narrowed towards the constriction, circular in section, rounded below. Sculpture. Radial ribs densely placed near the apex, moderately spaced and rather low on the upper body whorl (approximately (8–11 ribs/0.5 mm), moderately spaced on the lower body whorl but almost absent over the area of the constriction, and moderately spaced and somewhat more prominent on the tuba. Spiral striation fine. Aperture tilted approximately 70° relative to the coiling axis of the body whorls, with the upper margin at most level with the apex, widely ovate, teeth absent; inner peristome thickened, somewhat spreading; outer peristome distinctly flaring on the palatal side. Dimensions. Height of spire without tuba 0.8–0.9 mm; width c. 0.8 mm; ratio height/width 1.0–1.2; umbilicus open, up to 0.1 mm wide; number of whorls 3 1/4–3 1/2, excluding a tuba of approx. 1/2 whorl; height of aperture 0.5–0.6 mm; width of aperture c. 0.5 mm.

Distribution in Sabah. Widespread but rare: Mount Kinabalu, Pun Batu. Elevation range: 500–1100 m. In disturbed rainforest and shrubby woodland on limestone and sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Opisthostoma devogelii Vermeulen, 1991 (Sarawak), also has an upturned aperture

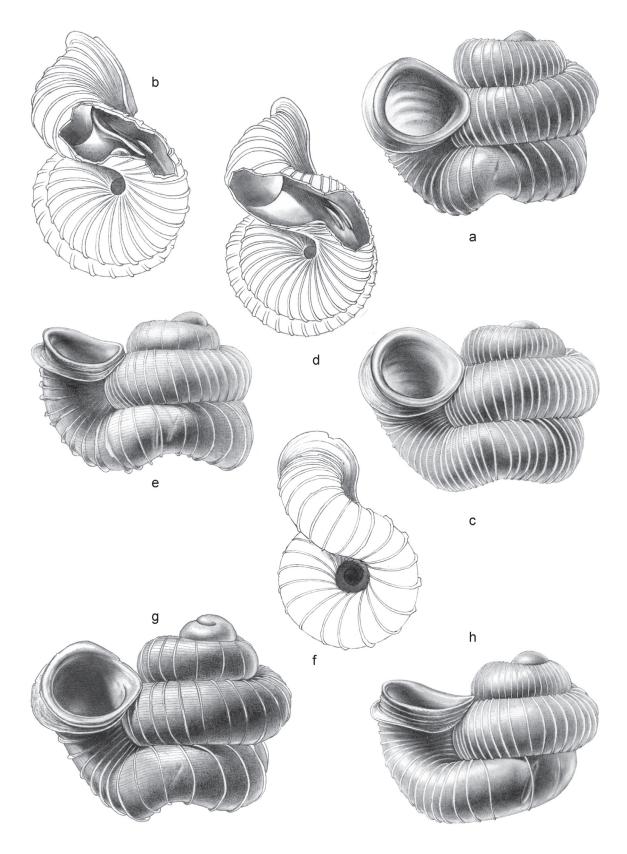


Fig. 56, a–d. *Opisthostoma brachyacrum lambii* (Vermeulen, 1991), a. Frontal view, shell 0.95 mm high, b. Umbilical view, part of the shell removed to show teeth in the constriction, c. Frontal view, shell 0.75 mm high, d. Umbilical view, part of the shell removed to show teeth in the constriction; e–g. *Opisthostoma javanicum* Van Benthem Jutting, 1932, e. Frontal view, shell 0.85 mm high, f. Umbilical view, part of the shell removed to show teeth in the constriction, g. Frontal view, shell 1.05 mm high; h. *Opisthostoma lechria* Vermeulen, 1991, frontal view, shell 0.90 mm high.

but has the last whorl before the start of the tuba not or hardly turned inwards.

Genus *Plectostoma* H Adams, 1865

Diagnosis for the Sabah species. Shell yellow to orange to brown. Tuba coiled around an axis which runs at a distinct angle to the axis of the spire. Aperture tilted up to 90° relative to the coiling axis of the spire (in *P. aversum* up to 135°). Spire (excluding tuba) with 45/8-71/2 whorls.

KEY TO THE GROUPS

1 – Constriction without a longitudinal palatalis

- Group 1
- 1 Constriction with a longitudinal palatalis (check carefully, it may be partly hidden under the suture)
 - 2 Radial ribs half-way along the tuba, on its lower surface, either with a deep, semicircular loop, or with a deeply trough-shaped projection, abrading to a scar with a deep, semi-circular loop **Group 2**
 - 2 Radial ribs half-way along the tuba, on its lower surface, either not sinuous, or sinuous, or with a shallow loop, or with a shallowly concave projection, abrading to a sinuous or shallowly looped scar
 - 3 Constriction without a longitudinal parietalis

Group 3

- 3 Constriction with a longitudinal parietalis
 - 4 Constriction without a basalis

Group 4

4 – Constriction with a basalis in the shape of a knob or a thickened transverse ridge (in the latter case often fused to the columellaris with the demarcation visible as a shallow depression) **Group 5**

Group 1

Check also:

Plectostoma dormani (Group 3). Shares the sinuous or looped radial ribs on the spire with *P. cyrtopleuron* and *P. perspectivum*, differs from Sabah material of the first by the absence of a columellaris in the constriction; from the second by the absence of a winged outer peristome.

Plectostoma cyrtopleuron (Vermeulen, 1994)

(fig. 57a–f, map 10f)

Opisthostoma cyrtopleuron Vermeulen 1994: 126; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Pun Batu approximately 30 km W of Sapulut.

Diagnosis. Differs from *Plectostoma immunitum* and *P. urunense* by the wider umbilicus (0.25–0.40 mm versus 0.10–0.20 mm), and by the larger aperture (height 0.6–0.8 mm versus 0.4–0.5 mm). Also, the radial ribs on the spire are usually slightly sinuous (but see note).

Description. Spire conical with straight to concave sides. Apex slightly oblique or not. Whorls convex; last whorl rounded to slightly angular at the periphery, slightly convex above and below. Constriction with 1–3 teeth: With or without 1 parietalis, with 1 transverse palatalis, with 1 inconspicuous to distinct columellaris (often lacking in Sarawak specimens). Tuba free from the spire, gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire rather closely placed to widely spaced (3–6 ribs/0.5 mm on the penultimate whorl), (slightly) sinuous, sometimes flattened and inconspicuous on the upper half of the whorls; radial ribs on the tuba widely spaced (2–3 ribs/0.5 mm half-way), sinuous below or not, or with a shallowly concave to deeply trough-shaped projection, abrading to a scar with a shallow to deep, semi-circular loop. Spiral striation present, sometimes fine. Aperture tilted up to 30° relative to the coiling axis of the spire, its upper margin well below the level of the apex, circular to elliptic. Peristome double, outer peristome slightly to distinctly spreading beyond the inner, but gradually narrowed towards, and absent along the right side of the aperture, often slightly to distinctly widened along the upper side; inner peristome slightly to distinctly protruding from the outer, (moderately) spreading. Dimensions. Height of spire without tuba 1.7–2.5 mm; width 1.2–1.6 mm; ratio height/width 1.3–1.7; width including tuba 2.6–3.1 mm; umbilicus 0.25–0.40 mm wide; number of whorls 5 1/8–6 3/4, excluding the tuba; height and width aperture 0.6–0.8 mm.

Distribution in Sabah. Widespread but rare: Balambangan island, Pun Batu, Sapulut. Elevation range: 0–600 m. In (disturbed) primary forest and shrub vegetation on limestone bedrock. Also in Sarawak. Endemic to Borneo. Variability. 1.Sabah populations vary in the shape of the spire, shape of the radial ribs, a more widely flaring outer peristome, as well as a distinctly protruding inner peristome.

2. A population from Balambangan island has most radial ribs approx. straight, with only a few slightly sinuous. Therefore, the key in Vermeulen (1994) identifies this as *Plectostoma wilfordi* (Vermeulen, 1994); however, the Balambangan shells are larger (spire around 2.2–2.5 mm high, versus 1.4–1.8 mm high) for which reason we feel they better fit in *P. cyrtopleuron*.

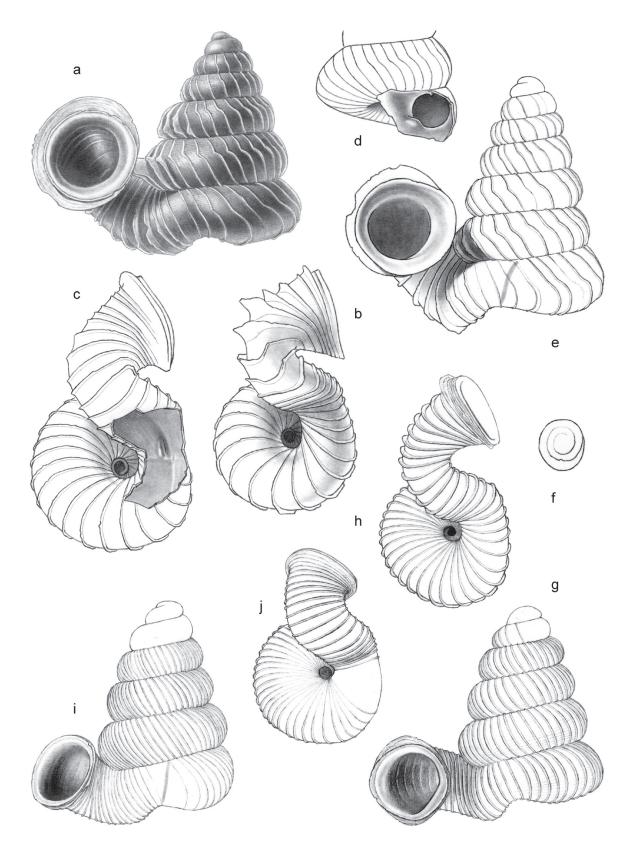


Fig. 57, a–f. *Plectostoma cyrtopleuron* (Vermeulen, 1994), a. Frontal view, shell 2.4 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction e. Frontal view, shell 2.7 mm high, f. Operculum; g–h. *Plectostoma immunitum* Vermeulen & Liew, new species, g. Frontal view, shell 1.8 mm high, h. Umbilical view; i–j. *Plectostoma urunense* Vermeulen & Liew, new species, i. Frontal view, shell 1.9 mm high, j. Umbilical view.

Plectostoma immunitum Vermeulen & Liew, new species

(fig. 57g-h, map 10f)

Type specimens from Malaysia, Sabah, Pinangah valley, Batu Urun (holotype BOR/MOL 14844; paratypes JV 7991/2 shells).

Diagnosis. Within Group 1, it shares the straight (not sinuous) radial ribs on the spire with sympatric *Plectostoma urunense*. It differs by the more widely spaced radial ribs (7–9 ribs/0.5 mm versus 10–14 ribs/0.5 mm on the penultimate whorl), by the aperture which is distant from the spire, by the outer peristome which distinctly spreads beyond the inner on the palatal side, and by the wider umbilicus (0.18–0.20 mm wide, versus 0.10 mm wide). Also resembling *P. inornatum*, see Group 3 and Group 4, differs by its smaller size (spire height 1.6–1.8 mm versus 2.2–2.5 mm) and by the absence of a longitudinal palatalis.

Description. Spire conical with approx. straight sides. Apex not oblique. Whorls distinctly convex; last whorl rounded. Constriction with 1 tooth: A (slight), knob-shaped columellaris. Tuba only proximally attached to the spire, gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire moderately spaced (7–9 ribs/0.5 mm on the penultimate whorl), not sinuous; those on the tuba slightly more spaced (4–6 ribs/0.5 mm half-way), not sinuous. Spiral striation present, fine and inconspicuous. Aperture distant from the spire, not or hardly tilted relative to the coiling axis of the spire, its upper margin well below the level of the apex, circular. Peristome double, outer peristome spreading beyond the inner but gradually narrowed towards the right side of the aperture, and there absent to narrow; inner peristome moderately protruding from the outer on the palatal side, slightly spreading. Dimensions. Height of spire without tuba 1.6–1.8 mm; width 1.1–1.2 mm; ratio height/ width 1.5–1.6; width including tuba 1.9–2.0 mm; umbilicus 0.18–0.20 mm wide; number of whorls 5 3/8–5 7/8, excluding the tuba; height and width aperture 0.45–0.50 mm.

Distribution in Sabah. Sinobang only. Elevation range: 300–500 m. Damp primary and secondary forest on limestone bedrock. Endemic to Sabah.

Name derivation. From immunitus (Latin) = unprotected, referring to the small number of teeth in the constriction.

Plectostoma perspectivum (Vermeulen, 1994)

(fig. 58a-c, map 11a)

Opisthostoma perspectivum Vermeulen 1994: 116; Clements et al. 2008: 2762. – Malaysia, Sabah, Interior Prov., Batu Punggol SE of Sapulut.

Cross diagnosis. Identified within Group 1 by the upper margin of the peristome, which is about level with the apex of the spire, or above this, and by the distinctly flaring outer peristome.

Description. Spire conical with about straight sides. Apex slightly oblique or not. Whorls moderately convex; last whorl rounded to slightly angular. Constriction with 3 teeth: 1 short, sometimes inconspicuous parietalis; 1 transverse palatalis; 1 small columellaris. Tuba gradually narrowed towards the constriction, rounded or slightly angular below. Sculpture. Radial ribs widely spaced (1-2 ribs/0.5 mm on the penultimate whorl and half-way on the tuba), on the spire with a shallowly concave to deeply trough-shaped projection on the lower half of the whorls, abrading to a sinuous or deeply looped scar; but those close to the tuba with a deeply trough-shaped projection on the periphery, abrading to a scar with a single deep loop when the shell is observed in front view; radial ribs on the tuba with an almost tubular, curved projection below, with a slightly inflated apex, abrading to a scar with a single deep loop. Spiral striation absent, rarely inconspicuous. Aperture tilted up to 45° relative to the coiling axis, its upper margin about level with the apex or widely above it, circular to elliptic. Peristome distant from the spire, double; outer peristome narrowed towards the right and lower side of the aperture, and there absent, along the upper side with a widely projecting, large, widely rounded wing which has (strongly) recurved margins and is often truncated to its right side; inner peristome distinctly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.7-2.0 mm; width 1.3-1.5 mm; ratio height/width 1.3-1.4; width including tuba 2.5-3.0 mm; umbilicus 0.40-0.55 mm wide; number of whorls 5 1/8-5 5/8, excluding the tuba; height and width aperture 0.6–0.7 mm.

Distribution in Sabah. Sapulut only. Elevation range: 300–400 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Plectostoma urunense Vermeulen & Liew, new species

(fig. 57i–j, map 11b)

Type specimens from Malaysia, Sabah, Sapulut valley, Temurung (holotype BOR/MOL 464) Pinangah valley, Sinobang (Batu Urun) (paratypes JV 18105/2 shells).

Diagnosis. Differs from sympatric Plectostoma immunitum by the more densely placed radial ribs (10–14 ribs/0.5 mm versus 7–9 ribs/0.5 mm on the penultimate whorl), by the aperture close to the spire, by the outer

peristome which spreads only slightly beyond the inner on the palatal side, and by the narrower umbilicus (0.10 mm wide, versus 0.18–0.20 mm wide).

Description. Spire conical with approx. straight sides. Apex not oblique. Whorls distinctly convex; last whorl rounded. Constriction with 1 tooth: A knob-shaped parietalis. Tuba only proximally attached to the spire, gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire rather densely placed (10–14 ribs/0.5 mm on the penultimate whorl), not sinuous; those on the tuba slightly more spaced (8–9 ribs/0.5 mm half-way), not sinuous. Spiral striation locally present, fine and inconspicuous. Aperture close to the spire, tilted c. 30° relative to the coiling axis of the spire, its upper margin well below the level of the apex, circular. Peristome double; outer peristome slightly spreading beyond the inner but gradually narrowed towards the right side of the aperture, and there absent to narrow; inner peristome slightly protruding from the outer, slightly spreading. Dimensions. Height of spire without tuba 1.7–1.8 mm; width c. 1.1 mm; ratio height/width c. 1.6; width including tuba 1.5–1.6 mm; umbilicus c. 0.10 mm wide; number of whorls 5 1/2–5 5/8, excluding the tuba; height and width aperture 0.40–0.45 mm.

Distribution in Sabah. Rare in S: Sinobang, Sapulut. Elevation range: 300–500 m. Damp primary and secondary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Resembles *Plectostoma baritense* (E A Smith, 1893) from Sarawak, differs by the approx. straight (versus approx. convex) sides of the spire, by the narrower umbilicus (c. 0.10 mm wide versus 0.15–0.20 mm wide), and by the absence of a longitudinal palatalis in the constriction. Also reminiscent of *P. aethoderma* (Vermeulen, 1994) from Sarawak, differs by its smaller size (spire height 1.7–1.8 mm, versus 2.0–3.1 mm) and the double peristome.

Name derivation. Named after the type locality, Batu Urun.

Group 2

Check also:

Plectostoma dormani (Group 3). Within Group 2 particularly resembling P. concinnum and P. lissopleuron. Differs from all species in Group 2 by the absence of a distinct parietalis

Plectostoma aversum Vermeulen & Liew, new species

(fig. 58d-g, map 11a)

Type specimens from Malaysia, Sabah, Baturong-Madai F.R., Madai hill (holotype BOR/MOL 14843; paratypes V 7691/26 shells).

Diagnosis. Identified among Borneo *Plectostoma* by the tilt of the aperture: It is averted from the observer if the shell is viewed frontally (= with the tuba to the left). If measured as in the other species, the aperture is tilted 90–135° relative to the coiling axis of the spire.

Description. Spire conical with approx. straight sides. Apex slightly oblique. Whorls convex; last whorl rounded. Constriction with 4 teeth: 1 parietalis; 1 longitudinal palatalis; 1 columellaris; 1 slight to distinct, knob-shaped basalis. Tuba gradually narrowed towards the constriction, angular and with a distinct ridge below. Sculpture. Radial ribs on the spire rather widely spaced (3–4 ribs/0.5 mm on the penultimate whorl), slightly sinuous or not, those close to the tuba not sinuous; radial ribs on the tuba widely spaced (2–4 ribs/0.5 mm half-way), below with a short, deeply trough-shaped projection abrading to a scar with a deep, semi-circular loop. Spiral striation locally present, fine. Aperture tilted 90–135° relative to the coiling axis of the spire (therefore averted if the shell is observed frontally), circular. Peristome double, outer peristome spreading beyond the inner but gradually narrowed towards, and absent to narrow along the right side of the aperture; inner peristome hardly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.6–2.1 mm; width 1.3–1.6 mm; ratio height/width 1.1–1.4; width including tuba 2.5–2.9 mm; umbilicus 0.30–0.40 mm wide; number of whorls 5 1/8–5 5/8, excluding the tuba; height aperture 0.5–0.55 mm; width aperture 0.55–0.6 mm.

Distribution in Sabah. Rare in E: Ulu Segama, Baturong-Madai. Elevation range: 100–200 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Name derivation. From aversus (Latin) = facing away.

Plectostoma concinnum (Fulton, 1901)

(fig. 59e-h, map 11b)

Opisthostoma concinnum Fulton 1901: 242; Zilch 1953a: 17; Vermeulen 1994: 105; Schilthuizen et al. 2006: 1851; Clements et al. 2008: 2762; Uchida et al. 2013: 52, 53. – Opisthostoma (Geothauma) concinnum (Fulton) Von Martens 1908: 258. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Opisthostoma smithi Fulton 1901: 243; Zilch 1953a: 17. - Opisthostoma (Plectostoma) smithi (Fulton) Kobelt

1902: 417. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

Description. Spire conical with straight to concave sides. Apex not oblique. Whorls moderately convex; last whorl (slightly) angular. Constriction with 4-5 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris; with or without 1 basalis that is knob-shaped or a transverse ridge. Tuba gradually narrowed towards the constriction, (slightly) angular or with a ridge below. Sculpture. Radial ribs on the spire rather closely placed to widely spaced (2-6 ribs/0.5 mm on the penultimate whorl), with a (shallowly) concave to deeply trough-shaped projection half-way, often abraded to a sinuous or shallowly to deeply looped scar, projection of those close to the tuba often double-channeled, either with both channels equally deep or with the upper channel much deeper than the lower, abrading to a scar with either a single or a double, deep or shallow loop when the shell is observed in front view; radial ribs on the tuba moderately to widely spaced (2-3 ribs/0.5 mm half-way along the tuba), below with a deeply trough-shaped, slightly curved projection abrading to a scar with a deep, semi-circular loop. Spiral striation fine. Aperture tilted up to 30° relative to the coiling axis of the spire, circular. Peristome double; outer peristome spreading beyond the inner but gradually narrowed towards the right side of the aperture, and there absent to narrow, often somewhat widened along the upper side; inner peristome hardly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.7–2.3 mm; width 1.3–1.5 mm; ratio height/width 1.3–1.7; width including tuba 2.5-3.2 mm; umbilicus 0.30-0.40 mm wide; number of whorls 5 1/2-6 3/8, excluding the tuba; height and width aperture 0.6–0.7 mm.

Distribution in Sabah. Locally common in E: Lower Kinabatangan; elsewhere rare: Banggi island (old record), Segaliud Lokan, Baturong-Madai. Elevation range: 0–300 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Variability. Populations from the Kinabatangan river valley are variable. In shape, localized populations approach other species which are endemic to the Kinabatangan river valley: Plectostoma fraternum, P. mirabile (both this group) and P. simplex (Group 5); see Schilthuizen et al. 2006 fig. 1. However, where P. concinnum lives sympatrically with these, separation based on morphology is usually easy, P. simplex sometimes excepted (see note under that species). Based on molecular phylogeny, Schilthuizen et al. (2006) include all four in a single species complex without formally proposing an alternative taxonomy. The two major clades in the phylogenetic tree are allopatric but are not supported by any characters. We apply the taxonomy of Vermeulen 1994 which recognizes morphologically distinct forms as separate species. The disadvantage is that this leaves P. concinnum as a paraphyletic unit.

Plectostoma fraternum (E A Smith, 1905)

(fig. 59a–d, map 11a)

Opisthostoma fraternum Smith 1905: 360; Vermeulen 1994: 105; Schilthuizen et al. 2006: 1851; Clements et al. 2008: 2762. — Opisthostoma (Plectostoma) fraternum (E A Smith) Von Martens 1908: 257 — Type from Malaysia, Sabah, 'northern parts of Borneo'.

Cross diagnosis. Similar to Plectostoma concinnum, P. dormani and P. lissopleuron, differs from all three by the outer peristome, which is continuous around the inner, and is distinctly protruding beyond the inner on the right side of the aperture (absent or continuous but very narrow in the other species mentioned). It also has more convex sides of the spire, the last part of the last whorl is more rounded, and the radial ribs on the spire are more widely spaced (1–2 ribs/0.5 mm, versus 2–8 ribs/0.5 mm). Also, P. fraternum lacks all spiral striation (fine or inconspicuous in the other species).

Description. Spire conical with slightly convex sides. Apex slightly oblique. Whorls convex; last whorl rounded or slightly angular. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire widely spaced (1–2 ribs/0.5 mm on the penultimate whorl), with a deeply trough-shaped projection half-way, abrading to a scar with a deep, semi-circular loop, projection of those close to the tuba double-channeled, either with both channels equally deep or with the upper channel much deeper than the lower, abrading to a scar with a single deep loop when the shell is observed in front view; radial ribs on the tuba widely spaced (c. 1 rib/0.5 mm half-way along the tuba), with a curved, deeply trough-shaped projection below, abrading to a scar with a deep, semi-circular loop. Spiral striation inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire, circular. Peristome distant from the spire, double; outer peristome spreading beyond the inner all around, though gradually somewhat narrowed along the right side of the aperture, somewhat widened along the upper side; inner peristome hardly protruding from the outer, spreading. Dimensions. Height of spire without tuba 2.1–2.4 mm; width 1.5–1.6 mm; ratio height/width 1.4–1.5; width including tuba 2.8–3.0 mm; umbilicus 0.20 mm wide; number of whorls 5 5/8–6 1/8, excluding the tuba; height and width aperture 0.6–0.8 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

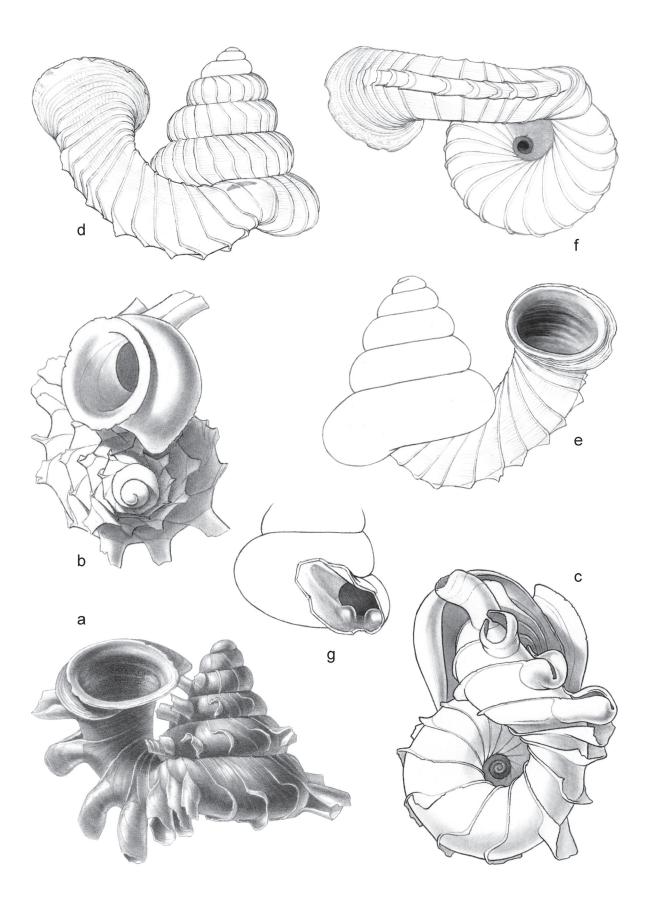


Fig. 58, a–c. *Plectostoma perspectivum* (Vermeulen, 1994), a. Frontal view, shell 1.8 mm high, b. Apical view, c. Umbilical view; d–g. *Plectostoma aversum* Vermeulen & Liew, new species, d. Frontal view, shell 1.8 mm high, e. Back view, f. Umbilical view, g. Left lateral view with tuba removed to show inner surface.

Note. Part of the *Plectostoma concinnum* species complex according to Schilthuizen et al. (2006); see note under *P. concinnum*.

Plectostoma lissopleuron lissopleuron (Vermeulen, 1994)

(fig. 60a–g, map 11b)

Opisthostoma lissopleuron lissopleuron Vermeulen 1994: 114; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Uchida et al. 2013: 52, 53. – Type from Malaysia, Sabah, Tawau Prov., Segarong hills 25 km ESE of Kunak, Pababola hill.

Opisthostoma decrespignyi auct. Saul 1967: 110.

[Not Opisthostoma decrespignyi H Adams].

Cross diagnosis. Plectostoma lissopleuron resembles *P. concinnum*; it differs by the radial ribs on the last half-whorl of the spire, which usually do not have a projection half-way, or an inconspicuous one only, nor an eroded crest (versus the presence of a projection half-way, often abraded to a scar with an unevenly eroded crest).

Description. Spire conical with concave to slightly convex sides. Apex slightly oblique or not. Whorls convex; last whorl rounded to slightly angular. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris which continues as a knob- to ridge-shaped transverse basalis. Tuba gradually narrowed towards the constriction, rounded to angular below. Sculpture. Radial ribs on the spire closely placed to moderately spaced (3–8 ribs/0.5 mm on the penultimate whorl), usually without a projection half-way, or with a slight one only, sinuous or not; radial ribs on the tuba closely placed to moderately spaced (3–6 ribs/0.5 mm half-way), sinuous or with a shallow to deep, semi-circular loop below, and sometimes with a short projection. Spiral striation inconspicuous to distinct. Aperture tilted up to 45° relative to the coiling axis of the spire, circular to elliptic. Peristome distant from the spire, double; outer peristome hardly to distinctly spreading beyond the inner, gradually narrowed towards, and absent or very narrow along the right side of the aperture, often with a widely rounded wing along the upper side of the aperture, and sometimes with a similar but less conspicuous wing along the lower side; inner peristome hardly to moderately protruding from the outer, at most with inconspicuous lamellae on its outer surface, spreading. Dimensions. Height of spire without tuba 1.7–2.4 mm; width 1.1–1.6 mm; ratio height/ width 1.3–1.7; width including tuba 2.2–3.2 mm; umbilicus 0.35–0.55 mm wide; number of whorls 5 3/8–6 7/8, excluding the tuba; height and width aperture 0.5–0.7 mm.

Distribution in Sabah. Scattered localities in E, S of lower Kinabatangan. Elevation range: 0–200 m. Primary and secondary forest on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Variability. Consists of well-isolated populations, each slightly different from the others, but each showing variability to such an extent that overlap in characters exists with other populations.

Plectostoma lissopleuron bigibbum (Vermeulen, 1994)

(fig. 61a–e, map 11c)

Opisthostoma lissopleuron bigibbum Vermeulen 1994: 115. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Madai hill, 40 km SSW of Lahad Datu.

Cross diagnosis. Differs from *Plectostoma lissopleuron lissopleuron* by the constriction with a distinct, knob-shaped transverse basalis, and the outer peristome which not or hardly spreads beyond the inner (although sometimes slightly widened along the upper side of the aperture) (The type subspecies either has a constriction with a ridge-shaped transverse basalis, or a constriction with a knob-shaped transverse basalis, but in such shells the outer peristome distinctly spreads beyond the inner).

Description. As the type subspecies, but spire with slightly concave to convex sides. Constriction with a distinctly knob-shaped basalis. Sculpture. Radial ribs on the spire rather closely placed to moderately spaced (3–6 ribs/0.5 mm on the penultimate whorl), slightly sinuous, but those close to the tuba often not or hardly sinuous; radial ribs on the tuba moderately to widely spaced (2–4 ribs/0.5 mm half-way), below with a shallow semi-circular loop. Aperture tilted up to 80° relative to the coiling axis of the spire. Peristome (widely) distant from the spire, outer peristome somewhat spreading beyond the inner or not, sometimes slightly widened along the upper side of the aperture; inner peristome hardly protruding from the outer. Dimensions. Height of spire without tuba 1.6–2.1 mm; width 1.2–1.4 mm; ratio height/width 1.2–1.5; width including tuba 2.0–2.6 mm; umbilicus 0.30–0.40 mm wide; height and width aperture 0.5–0.7 mm.

Distribution in Sabah. Rare in E: Tabin, Baturong-Madai. Elevation range: 100–200 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Note. Large series of shells can easily be distinguished from subsp. *lissopleuron*; single shells are sometimes difficult to identify, particularly if they are slightly worn.

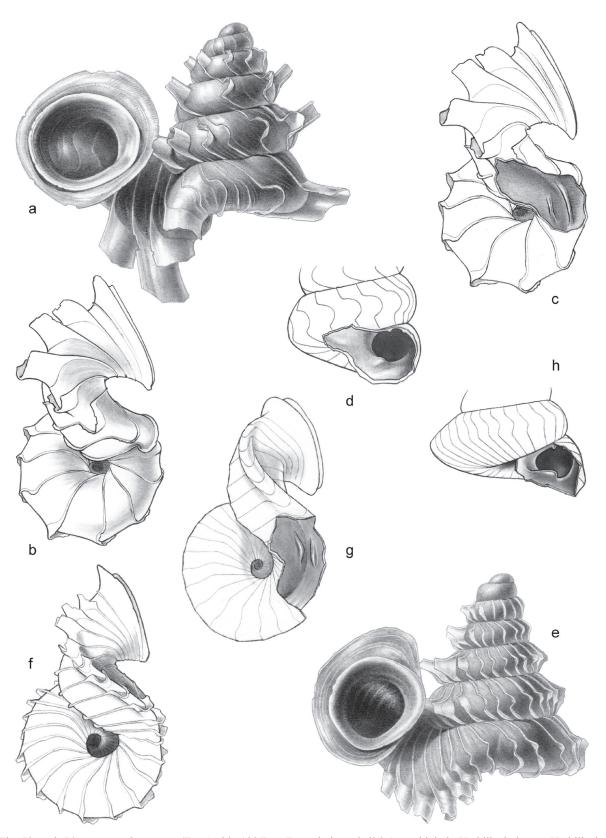


Fig. 59, a–d. *Plectostoma fraternum* (E A Smith, 1905), a. Frontal view, shell 2.1 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction; e–h. *Plectostoma concinnum* (Fulton, 1901), e. Frontal view, shell 2.4 mm high, f. Umbilical view, g. Umbilical view, part of the shell removed to show teeth in the constriction, h. Left lateral view with tuba removed to show inner surface of constriction.

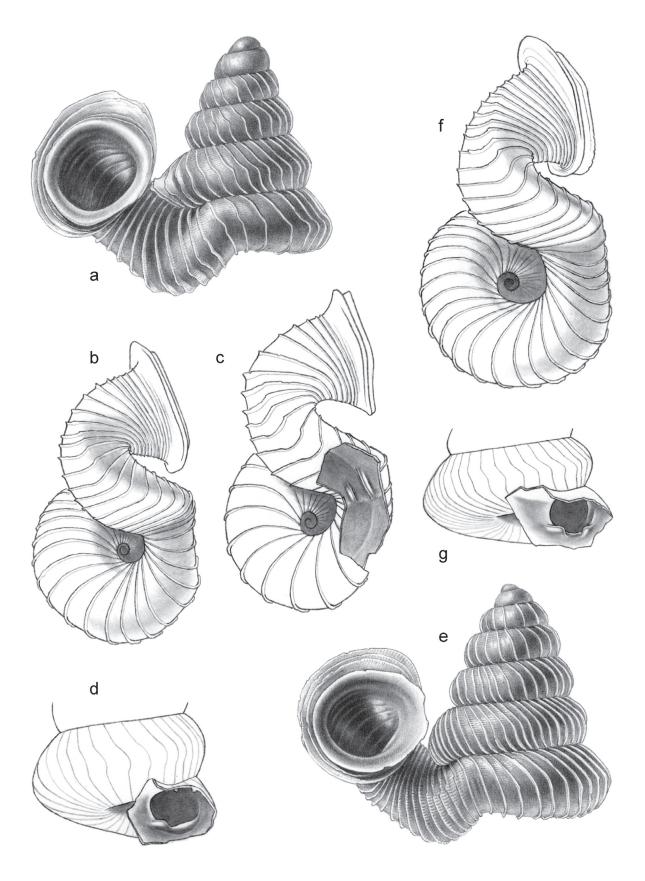


Fig. 60, a–g. *Plectostoma lissopleuron* (Vermeulen, 1994), a. Frontal view, shell 2.1 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction; e. Frontal view, shell 2.4 mm high, f. Umbilical view, g. Left lateral view with tuba removed to show inner surface of constriction.

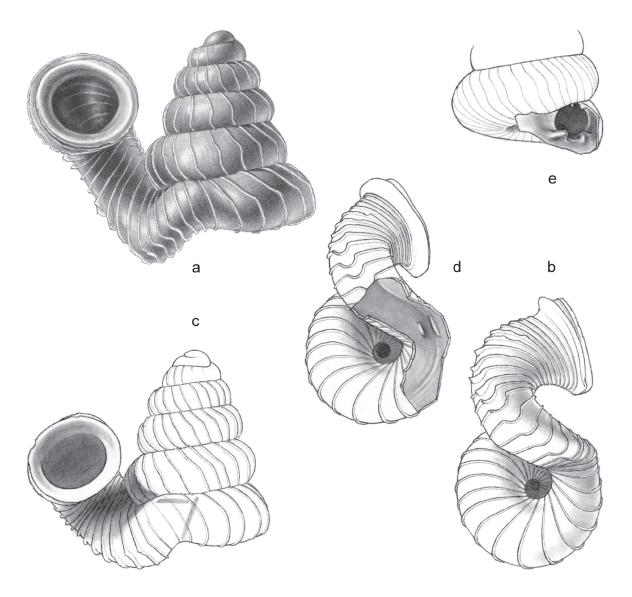


Fig. 61, a–e. *Plectostoma lissopleuron bigibbum* (Vermeulen, 1994), a. Frontal view, shell 2.1 mm high, b. Umbilical view, c. Frontal view, shell 2.0 mm high, d. Umbilical view, part of the shell removed to show teeth in the constriction, e. Left lateral view with tuba removed to show inner surface of constriction.

Plectostoma mirabile (E A Smith, 1893)

(fig. 62a–e, map 11c)

Opisthostoma mirabile Smith 1893b: 346; 1894a: 271; Saul 1967: 110; Vermeulen 1994: 104; Schilthuizen et al. 2006: 1851; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – Opisthostoma (Plectostoma) mirabile (Smith) Kobelt & Von Möllendorff 1898: 134. – Opisthostoma (Geothauma) mirabile (Smith) Kobelt 1902: 419; Von Martens 1908: 258. – Type from Malaysia, Sabah, 'Gomanton Hill'.

Cross diagnosis. Identified in Group 2 by the outer peristome with a distinct wing on the upper side.

Description. Spire conical with straight to concave sides. Apex not oblique. Whorls convex; last whorl rounded or slightly angular. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris which continues as a ridge-shaped transverse basalis. Tuba gradually narrowed towards the constriction, (slightly) angular below. Sculpture. Radial ribs on the spire moderately to widely spaced (2–4 ribs/0.5 mm on the penultimate whorl), with a deeply trough-shaped projection half-way, abrading to a scar with a deep, semi-circular loop, projection of those close to the tuba slightly double-channeled, abrading to a scar with a single deep loop when the shell is observed in front view; radial ribs on the tuba widely spaced (2 ribs/0.5 mm half-way along the

tuba), below with a distinctly curved projection abrading to a scar with a single deep loop. Spiral striation absent. Aperture tilted up to 30° relative to the coiling axis of the spire, circular to elliptic. Peristome double; outer peristome widely spreading beyond the inner but abruptly narrowed towards, and absent along the right side of the aperture, with a very large wing along the upper side; inner peristome distinctly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.8–3.1 mm; width 1.3–1.9 mm; ratio height/width 1.4–1.6; width including tuba 2.6–3.9 mm; umbilicus 0.20–0.30 mm wide; number of whorls 5 3/8–7 1/2, excluding the tuba; height aperture 0.5–0.7 mm; width 0.6–0.9 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–200 m. Disturbed primary forest on limestone bedrock. Endemic to Sabah.

Variability. Variable in the height of the spire as well as in the spacing of the ribs. An old sample from near Suanlamba consists of a series of rather small specimens with a wide spire with rather closely placed radial ribs. Similar specimens are sometimes found on small limestone outcrops near Gomantong hill, among specimens more closely resembling the type.

Note. Part of the *Plectostoma concinnum* species complex according to Schilthuizen et al. 2006; see note under *P. concinnum*.

Group 3

Check also:

Plectostoma obliquedentatum (Group 5). Shells without a longitudinal parietalis differ from *P. dormani* by the approx. straight (= without a loop) radial ribs on the tuba, from *P. inornatum* by the wider umbilicus (0.3–0.4 mm versus 0.20–0.25 mm), and from *P. otostoma* by the absence of a small wing on the outer peristome, on the upper side of the aperture.

Plectostoma dormani (Vermeulen, 1994)

(fig. 63a-h, map 11c)

Opisthostoma dormani Vermeulen 1994: 103; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Interior Prov., 1 km SE of Simatuoh, 10 km ESE of Sapulut.

Cross diagnosis. Differs from *Plectostoma inornatum* and *P. otostoma* by the radial ribs on the tuba, which leave a scar with a (moderately) deep loop.

Description. Spire conical with straight to concave sides. Apex not oblique. Whorls convex; last whorl rounded or slightly angular. Constriction with 1–2 teeth: With or without 1 longitudinal palatalis; 1 transverse palatalis. Tuba gradually narrowed towards the constriction, rounded to slightly angular below. Sculpture. Radial ribs on the spire moderately to widely spaced (2–5 ribs/0.5 mm on the penultimate whorl), with a shallowly concave to deeply trough-shaped projection half-way, abrading to a scar with a shallow to deep, semi-circular loop, but the projection of those close to the tuba double-channeled with the upper channel much deeper than the lower, abrading to a distinctly sinuous scar or a scar with a single deep loop when the shell is observed in front view); radial ribs on the tuba widely spaced (1-2 ribs/0.5 mm half-way along the tuba), on the lower side with a slightly curved projection abrading to a scar with a (moderately) deep loop. Spiral striation absent or inconspicuous. Aperture tilted up to 30° relative to the coiling axis of the spire, circular to elliptic. Peristome simple (because outer and inner peristome fused) or double; when simple spreading, often with a somewhat thickened lip inside; when double outer peristome somewhat spreading beyond the inner or not, if so, gradually narrowed towards the right side of the aperture, and there absent, often somewhat widened along the upper side; inner peristome usually not or hardly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.9–2.6 mm; width 1.3–1.6 mm; ratio height/width 1.3–1.7; width including tuba 2.5–2.9 mm; umbilicus 0.30–0.40 mm wide; number of whorls 5 3/8–7 1/8, excluding the tuba; height aperture 0.6–0.7 mm; width 0.6–0.8 mm.

Distribution in Sabah. Sapulut only. Elevation range: 300–500 m. In (disturbed) primary forest, on limestone bedrock. Endemic to Sabah.

Variability. Variable in the shallowly/deeply looped radial rib scars on the spire, in the presence/absence of spiral striation, in the presence/absence of a longitudinal palatalis in the constriction, and in the simple/double peristome. The states of these characters occur in all possible combinations; further division of *Plectostoma dormani* is therefore not possible.

Plectostoma inornatum (Vermeulen, 1994)

(fig. 64a–d, map 11d)

Opisthostoma inornatum Vermeulen 1994: 107. – Type from Malaysia, Sabah, Interior Prov., 1 km SE of Simatuoh, 10 km ESE of Sapulut.

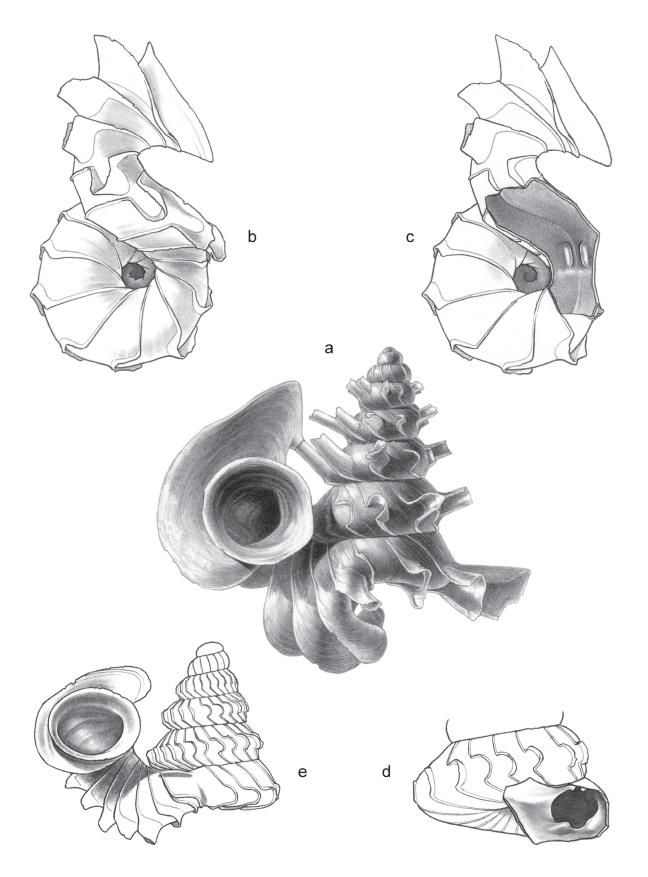


Fig. 62, a—e. *Plectostoma mirabile* (E A Smith, 1893), a. Frontal view, shell 3.3 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction, e. Frontal view, shell 2.1 mm high.

Description. Spire conical with straight to very slightly convex sides. Apex oblique or not. Whorls convex; last whorl rounded. Constriction with 2–4 teeth: With or without 1 parietalis, if present inconspicuous; 1 often inconspicuous longitudinal palatalis; 1 transverse palatalis; rarely with 1 very inconspicuous columellaris. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs closely placed to moderately spaced (5–10 ribs/0.5 mm on the spire, 5–8 ribs/0.5 mm half-way on the tuba), slightly sinuous or not, those close to the tuba and on the tuba not sinuous. Spiral striation present. Aperture hardly tilted relative to the coiling axis of the spire, circular. Peristome distant from the spire, double; outer peristome hardly to moderately spreading beyond the inner, but gradually narrowed towards the right side of the aperture, there narrow to almost absent, slightly widened or with an inconspicuous wing along the upper side, sometimes very slightly widened along the lower side; inner peristome slightly protruding from the outer, spreading. Dimensions. Height of spire without tuba 2.2–2.5 mm; width 1.3 mm; ratio height/width 1.7–1.9; width including tuba 2.5 mm; umbilicus 0.20–0.25 mm wide; number of whorls 6 1/8–6 7/8, excluding the tuba; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Widespread but rare: Kota Marudu, Sapulut. Elevation range: 0–600 m. In disturbed primary forest on limestone bedrock. Endemic to Sabah.

Variability. Variable in characters regarded as diagnostic in other species: Presence or absence of a parietalis; radial ribs straight or slightly sinuous.

Plectostoma otostoma (O Boettger, 1893)

(fig. 64e-h, map 10e)

Opisthostoma otostoma Boettger 1893: 194; Smith 1894a: 271; 1895: 118; Zilch 1953a: 16; Vermeulen 1994: 106. – Opisthostoma (Plectostoma) otostoma (O Boettger) Kobelt & Von Möllendorff 1898: 134; Kobelt 1902: 417; Von Martens 1908: 258; Clements et al. 2006: 738. – Type from Malaysia, 'Labuan'.

Cross diagnosis. Identified within Group 3, particularly *Plectostoma inornatum*, by the small wing on the outer peristome, along the upper side of the aperture.

Description. Spire conical with straight sides. Apex slightly oblique. Whorls convex; last whorl rounded. Constriction with 3 teeth: 1 longitudinal and 1 transverse palatalis, and 1 inconspicuous columellaris. Tuba somewhat abruptly narrowed towards the constriction, rounded. Sculpture. Radial ribs on the spire moderately spaced (3–4 ribs/0.5 mm on the penultimate whorl), slightly sinuous, those close to the tuba not sinuous; radial ribs on the tuba moderately spaced (c. 3 ribs/0.5 mm half-way along the tuba), not or slightly sinuous below. Spiral striation present. Aperture hardly tilted relative to the coiling axis of the spire, circular to elliptic. Peristome double; outer peristome spreading beyond the inner but gradually narrowed towards the right side of the aperture, and there absent, with a distinct, but small wing along the upper side which often has a somewhat concave right margin; inner peristome slightly protruding from the outer, spreading. Dimensions. Height of spire without tuba 2.0–2.2 mm; width 1.5–1.6 mm; ratio height/width 1.3–1.4; width including tuba 2.4–2.7 mm; umbilicus 0.15–0.30 mm wide; number of whorls 5 1/2–6 1/8, excluding the tuba; height aperture 0.6–0.7 mm; width 0.6 mm.

Distribution in Sabah. Labuan only (old records). Elevation range: 0–100 m. Coastal vegetation on limestone bedrock. Endemic to Sabah.

Group 4

Check also:

Plectostoma inornatum (Group 3). Within Group 4 characterized by the inconspicuous or absent columellaris in the constriction.

Plectostoma jucundum (Group 5). Within Group 4 characterized by the radial ribs on the spire which have a distinct projection half-way.

Plectostoma obliquedentatum (Group 5). Within Group 4 characterized by the oblique parietalis which crosses the suture, in the direction of the aperture, into a palatal position.

Plectostoma brevituba (Vermeulen, 1994)

(fig. 65a-e, map 11d)

Opisthostoma brevituba Vermeulen 1994: 109; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2762.
 Type from Malaysia, Sabah, Sandakan Prov., Agop Batu Tulug near road Lahad Datu-Sandakan, near Kinabatangan river.

Cross diagnosis. Within Group 4 characterized by the aperture, which is close to the spire, almost touching. Resembles *Plectostoma decrespignyi*, differs by the slightly more convex spire, by the outer peristome which is widened along the upper side of the aperture, and by the more distinctly protruding inner peristome.

Description. Spire conical with straight to convex sides. Apex slightly oblique or not. Whorls convex; last

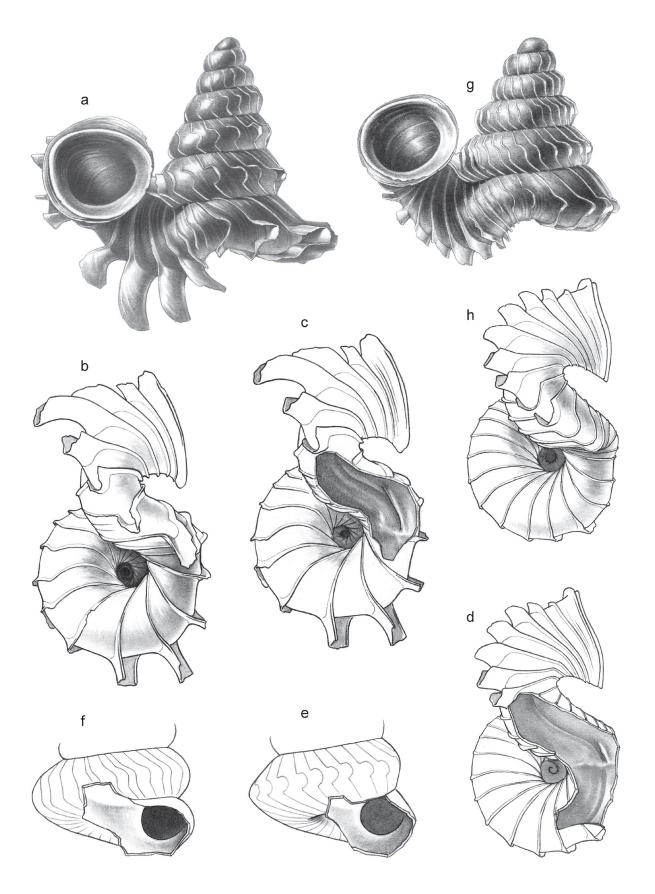


Fig. 63, a–h. *Plectostoma dormani* (Vermeulen, 1994), a. Frontal view, shell 2.5 mm high, b. Umbilical view, c, d. Umbilical view, part of the shell removed to show teeth in the constriction, e, f. Left lateral view with tuba removed to show inner surface of constriction g. Frontal view, shell 2.3 mm high, h. Umbilical view.

whorl rounded. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 distinct columellaris. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs (moderately) spaced (4–6 ribs/0.5 mm on the penultimate whorl and half-way on the tuba), not or hardly sinuous. Spiral striation fine. Aperture hardly tilted relative to the coiling axis of the spire, circular to elliptic, often slightly angular. Peristome almost touching the spire or somewhat distant from it, double; outer peristome slightly spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there narrow or absent, moderately widened or with a small wing along the upper side, and somewhat less widened along the lower side; inner peristome moderately protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.8–2.3 mm; width 1.3–1.5 mm; ratio height/width 1.3–1.6; width including tuba 2.2–2.4 mm; umbilicus 0.20–0.30 mm wide; number of whorls 5 1/4–6 1/4, excluding the tuba; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Rare in E: Lower Kinabatangan, Tabin. Elevation range: 0–100 m. In (disturbed) primary forest. Endemic to Sabah.

Plectostoma decrespignyi H Adams, 1865

(fig. 65f–h, map 11d)

H Adams 1865: 177 ('DeCrespignii'); Issel 1874: 439. – Opisthostoma decrespignyi (H Adams) Blanford 1867b: 305 ('DeCrespignii'); Tenison Woods 1888: 1071 ('crespignyi'); Godwin-Austen 1891: 350; Smith 1894a: 270; Vermeulen 1994: 110; Clements et al. 2006: 738. – Opisthostoma (Plectostoma) decrespignyi (H Adams) Kobelt & Von Möllendorff 1898: 134 ('crespignyi'); Kobelt 1902: 416; Von Martens 1908: 257. – Type from Malaysia, 'Labuan'.

Scoliostoma sp. De Crespigny 1865: 599.

[Not Opisthostoma decrespignyi auct. Saul 1967: 110; = Opisthostoma lissopleuron lissopleuron Vermeulen].

Description. Spire conical with straight to slightly concave sides. Apex slightly oblique or not. Whorls convex; last whorl rounded. Constriction with 4 teeth: 1 inconspicuous and often somewhat distorted parietalis; 1 similar longitudinal palatalis; 1 transverse palatalis; 1 knob-shaped columellaris which abruptly ends towards the basal side of the constriction. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs moderately spaced (4–6 ribs/0.5 mm on the penultimate whorl, 3–4 ribs/0.5 mm half-way on the tuba), not sinuous (rarely slightly so). Spiral striation fine. Aperture tilted up to 30° relative to the coiling axis of the spire, circular. Peristome (somewhat) distant from the spire, double; outer peristome hardly spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there absent or narrow, slightly widened along the upper side; inner peristome slightly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.7–1.9 mm; width 1.2–1.3 mm; ratio height/width 1.4–1.6; width including tuba 2.2–2.3 mm; umbilicus 0.25–0.35 mm wide; number of whorls 5 3/8–5 7/8, excluding the tuba; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Rare in W: Labuan (old records), Sinobang. Elevation range: 0–400 m. Damp primary forest on limestone bedrock. Endemic to Sabah.

Note. The spelling 'decrespignyi' has been used exclusively since 1902 and is therefore retained (ICZN art. 33.2.3.1).

Plectostoma depauperatum (E A Smith, 1894)

(fig. 66a–d, map 11e)

Opisthostoma depauperatum Smith 1894a: 272; Vermeulen 1994: 109. – Type from Sarawak, 'Barit mountain, NW Borneo'.

Cross diagnosis. Differs from *Plectostoma decrespignyi* by the slightly convex sides of the spire (or slightly convex close to the apex, and slightly concave lower down (versus flat or slightly concave). Also, the inner peristome is usually moderately protruding from the outer (usually slightly so in *P. decrespignyi*).

Description. Spire conical with slightly convex sides, or with convex sides near the apex, slightly concave lower down. Apex slightly oblique or not. Whorls convex; last whorl rounded. Constriction with 4 teeth: 1 parietalis, 1 longitudinal and 1 transverse palatalis, 1 distinct columellaris which abruptly ends towards the basal side of the constriction. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs (moderately) spaced (3–5 ribs/0.5 mm on the penultimate whorl, 3–4 ribs/0.5 mm half-way on the tuba), not or very slightly sinuous. Spiral striation absent or inconspicuous. Aperture hardly tilted relative to the coiling axis of the spire, circular, elliptic, or slightly angular. Peristome (widely) distant from the spire, rarely only slightly distant, double; outer peristome usually somewhat spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there absent, often slightly widened along the upper side; inner peristome usually moderately protruding from the outer, rarely only slightly protruding, spreading. Dimensions. Height of spire without tuba 1.5–2.3 mm; width 1.2–1.5 mm; ratio height/width 1.3-1.6; width including tuba 2.2–2.6 mm; umbilicus

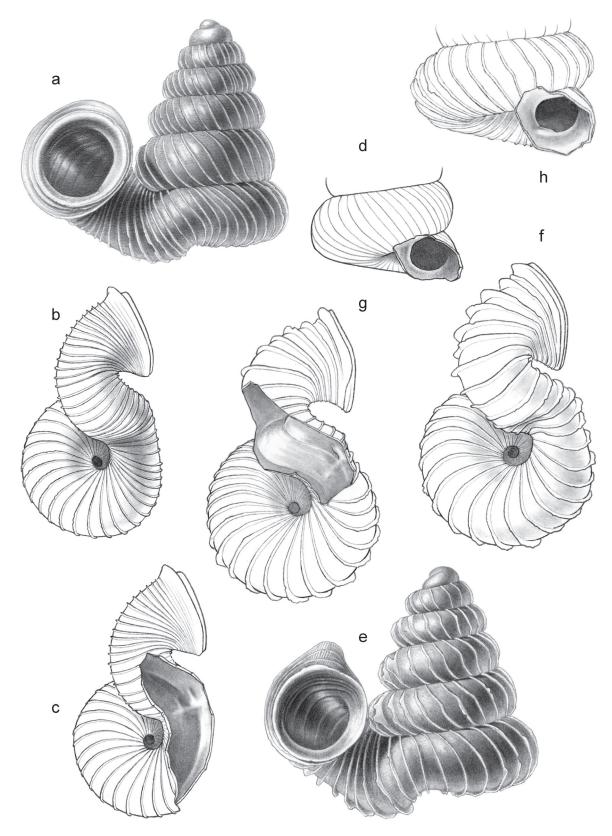


Fig. 64, a–d. *Plectostoma inornatum* (Vermeulen, 1994), a. Frontal view, shell 2.0 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction; e–h. *Plectostoma otostoma* (O Boettger, 1893), e. Frontal view, shell 2.4 mm high, f. Umbilical view, g. Umbilical view, part of the shell removed to show teeth in the constriction, h. Left lateral view with tuba removed to show inner surface of constriction.

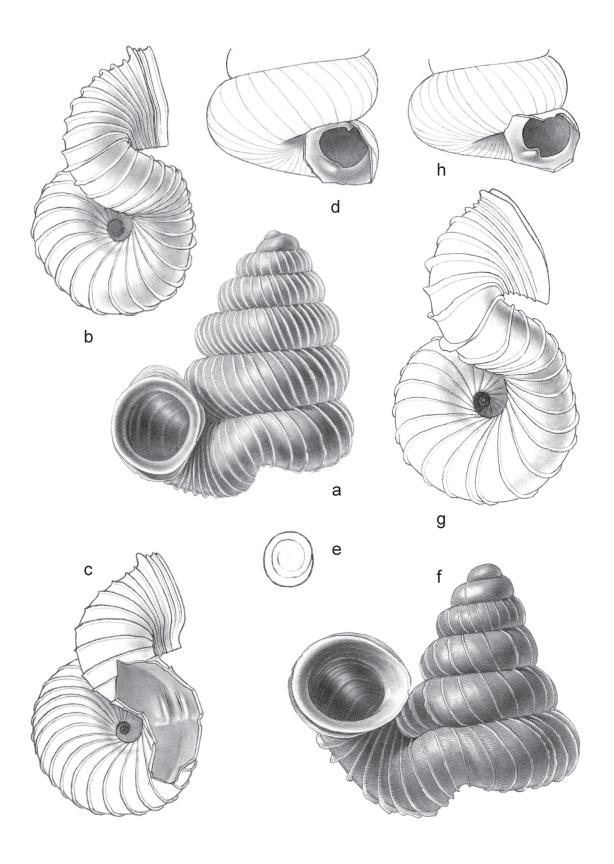


Fig. 65, a—e. *Plectostoma brevituba* (Vermeulen, 1994), a. Frontal view, shell 2.1 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction, e. Operculum; f—h. *Plectostoma decrespignyi* H Adams, 1865, f. Frontal view, shell 2.0 mm high, g. Umbilical view, h. Left lateral view with tuba removed to show inner surface of constriction.

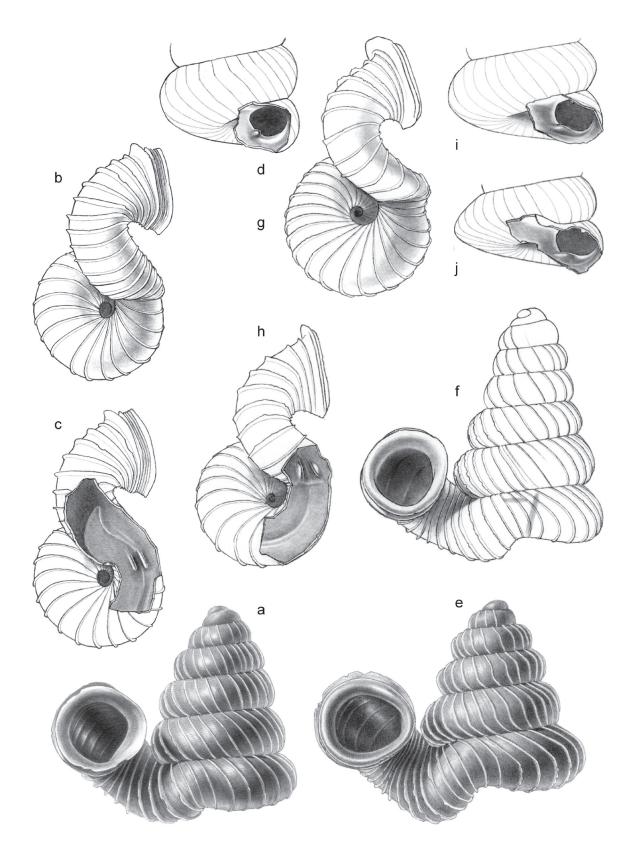


Fig. 66, a–d. *Plectostoma depauperatum* (E A Smith, 1894), a. Frontal view, shell 2.6 mm high, b. Umbilical view, c. Umbilical view, part of the shell removed to show teeth in the constriction, d. Left lateral view with tuba removed to show inner surface of constriction; e–j. *Plectostoma transequatorialis* (Vermeulen, 1994), e. Frontal view, shell 2.3 mm high, f. Frontal view, shell 2.5 mm high, g. Umbilical view, h. Umbilical view, part of the shell removed to show teeth in the constriction, i–j. Left lateral views with tuba removed to show inner surface of constriction.

open, 0.20–0.25 mm across; number of whorls 5 3/8–6 1/4, excluding tuba; height and width aperture 0.5–0.6 mm. *Distribution in Sabah*. Balambangan island only. Elevation range: 0–100 m. Dry, coastal primary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Variability. Shells may have a distinctly more elongated spire than the one depicted, as well as less conspicuous, more densely placed ribs.

Plectostoma transequatorialis (Vermeulen, 1994)

(fig. 66e–j, map 11e)

Opisthostoma transequatorialis Vermeulen 1994: 113. – Type from Indonesia, Kalimantan Selatan, mount Buleh 4 km E of Muara Uja.

Cross diagnosis. Differs from Plectostoma decrespignyi and P. depauperatum by the columellaris in the constriction, which gradually disappears towards the basal side of the constriction. It also differs from P. depauperatum by usually having a spire with straight to concave sides, and it differs from P. decrespignyi by its more distinct, sharply outlined longitudinal parietalis and palatalis.

Description. Spire conical with straight to concave sides, rarely with very slightly convex sides. Apex slightly oblique or not. Whorls convex; last whorl rounded or slightly angular. Constriction with 4 teeth: 1 sharply outlined parietalis, 1 similar longitudinal palatalis, 1 transverse palatalis, 1 columellaris which gradually disappears towards the basal side of the constriction. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire (moderately) spaced (3–5 ribs/0.5 mm on the penultimate whorl), (slightly) sinuous (rarely not so), radial ribs on the tuba moderately spaced (3–4 ribs/0.5 mm half-way on the tuba), not sinuous. Spiral striation fine. Aperture tilted up to 30° relative to the coiling axis of the spire, circular to subrectangular. Peristome distant from the spire, double; outer peristome hardly to moderately spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there absent or narrow, often slightly widened along the upper side; inner peristome slightly protruding (rarely moderately protruding) from the outer, spreading. Dimensions. Height of spire: Height 1.5–2.3 mm; width 0.9–1.5 mm; ratio height/width 1.3–1.7; width including tuba 1.7–3.0 mm; umbilicus open, 0.20–0.35 mm across; number of whorls 4 5/8–6 7/8, excluding tuba; height and width aperture 0.4–0.6 mm.

Distribution in Sabah. Widespread in S but rare: Bukit Melikop, Sinobang, Tun Sakaran Marine Park. Elevation range: 200–700 m. Primary forest on steep mountain slope, on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Group 5

Check also:

Plectostoma lissopleuron (Group 2). In Group 5 it resembles *P. simplex*; it differs by the less distinctly projecting outer peristome which, if with a slight wing along the upper side of the aperture, gradually narrows towards the right side of the aperture. Also, *P. simplex* usually has more distinct lamellae on the outer surface of the peristome.

Plectostoma bihamulatum (Vermeulen, 1994)

(fig. 67a–h, map 11e)

Opisthostoma bihamulatum Vermeulen 1994: 111. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong, 50 km WSW of Lahad Datu.

Cross diagnosis. Within Group 5 characterized by the two small projections on the outer peristome, along the left and upper side of the aperture, and by the narrow umbilicus (diameter 0.15–0.25 mm versus 0.30–0.40 mm).

Description. Spire conical with about straight sides. Apex (slightly) oblique. Whorls convex; last whorl rounded. Constriction with 4–5 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris; a knob- to ridge-shaped transverse basalis which is sometimes fused to the columellaris. Tuba gradually narrowed towards the constriction, rounded or slightly angular below. Sculpture. Radial ribs on the spire moderately to widely spaced (3–6 ribs/0.5 mm on the penultimate whorl), (hardly) sinuous, those close to the tuba not sinuous; radial ribs on the tuba often slightly more widely spaced (3–5 ribs/0.5 mm half-way along the tuba), not or slightly sinuous below. Spiral striation present, often inconspicuous. Aperture tilted up to 30° relative to the coiling axis of the spire, subrectangular to subtriangular. Peristome almost touching the spire or distant from it, double; outer peristome (somewhat) spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there absent, with an inconspicuous to distinct edge or a small projection along the left side and a (moderately) distinct edge or small, obtuse (rounded but not widely so) projection along the upper side; inner peristome protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.6–2.3 mm; width 1.2–1.5 mm; ratio height/width

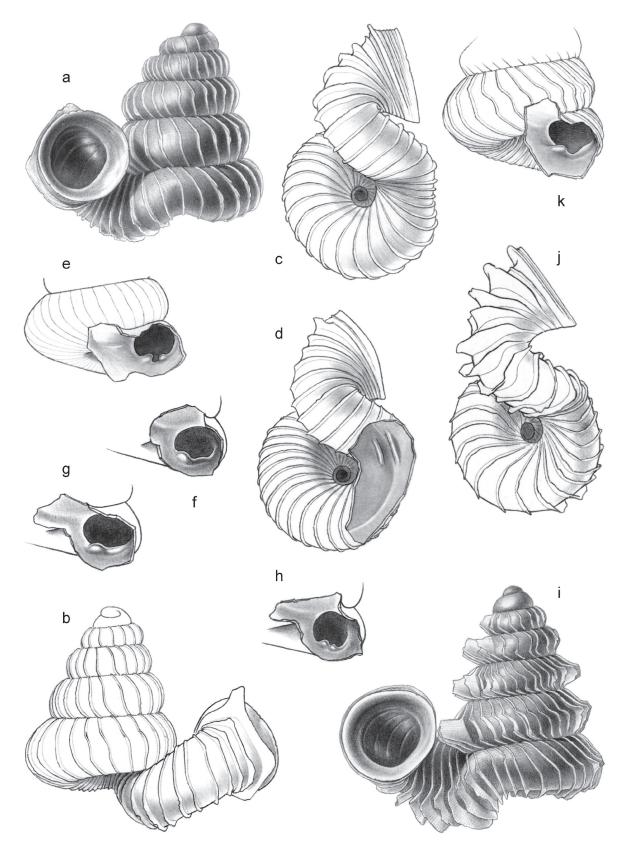


Fig. 67, a—h. *Plectostoma bihamulatum* (Vermeulen, 1994), a. Frontal view, shell 2.0 mm high, b. Back view, shell 2.0 mm high, c. Umbilical view, d. Umbilical view, part of the shell removed to show teeth in the constriction, e—h. Left lateral views with tuba removed to show inner surface of constriction; i—k. *Plectostoma jucundum* (E A Smith, 1893), i. Frontal view, shell 2.2 mm high, j. Umbilical view, k. Left lateral view with tuba removed to show inner surface of constriction.

1.2–1.7; width including tuba 2.0–2.7 mm; umbilicus 0.15–0.25 mm wide; number of whorls 5 3/8–6 3/8, excluding the tuba; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Rare in SE: Baturong-Madai, Tawau hills. Elevation range: 0–300 m. In disturbed primary forest on limestone bedrock. Endemic to Sabah.

Plectostoma jucundum (E A Smith, 1893)

(fig. 67i–k, map 11f)

Phung et al. 2017: 64. – Opisthostoma jucundum Smith 1893b: 347; 1894a: 271; Vermeulen 1994: 113; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data. – Opisthostoma (Plectostoma) jucundum (Smith) Kobelt & Von Möllendorff 1898: 134; Kobelt 1902: 417; Von Martens 1908: 257. – Type from Malaysia, Sabah, West Coast Prov., Mantanani islands.

Cross diagnosis. Within Group 5 characterized by the radial ribs on the spire which have a distinct projection half-way.

Description. Spire conical with straight sides. Apex slightly oblique or not. Whorls convex; last whorl rounded. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and a transverse palatalis; 1 columellaris which continues as a ridge-shaped transverse basalis. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire moderately to widely spaced (3–5 ribs/0.5 mm on the penultimate whorl), sinuous with a shallowly concave projection half-way, abrading to a sinuous scar; radial ribs on the tuba widely spaced (2–3 ribs/0.5 mm half-way), below slightly sinuous and with a shallowly concave projection, abrading to a not or slightly sinuous scar. Spiral striation distinct, rather coarse. Aperture hardly tilted relative to the coiling axis of the spire, circular to elliptic. Peristome distant from the spire, double; outer peristome only slightly spreading beyond the inner, but gradually narrowed towards the right side of the aperture, and there absent, sometimes slightly widened along the upper side; inner peristome slightly protruding from the outer, spreading. Dimensions. Height of spire without tuba 2.0–2.3 mm; width 1.4–1.5 mm; ratio height/width 1.4–1.5; width including tuba 2.5–2.8 mm; umbilicus 0.30–0.35 mm wide; number of whorls 5 7/8–6 1/8, excluding the tuba; height aperture 0.5–0.6 mm; width 0.6 mm.

Distribution in Sabah. Mantanani islands only. Elevation range: 0–100 m. In shrubby coastal vegetation on limestone bedrock. Endemic to Sabah.

Plectostoma obliquedentatum (Vermeulen, 1994)

(fig. 68a-e, map 11f)

Opisthostoma obliquedentatum Vermeulen 1994: 107; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data. – Type from Malaysia, Interior Prov., 4 km N of Simatuoh, 9 km NE of Sapulut.

Cross diagnosis. Within Group 5 characterized by the oblique parietalis which crosses the suture, in the direction of the aperture, into a palatal position.

Description. Spire conical with straight or slightly convex sides. Apex not or slightly oblique. Whorls convex; last whorl rounded. Constriction with 3–5 teeth: With or without 1 parietalis, if present inconspicuous, starting about half-way along the length of the longitudinal palatalis and obliquely crossing the suture and continuing into the tuba well beyond the longitudinal palatalis; with 1 longitudinal and 1 transverse palatalis; with or without 1 columellaris; with or without 1 ridge-shaped transverse basalis. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire moderately spaced (4–6 ribs/0.5 mm on the penultimate whorl), sinuous or not, those close to the tuba not or hardly sinuous; radial ribs on the tuba moderately to widely spaced (2–4 ribs/0.5 mm half-way), not or hardly sinuous below. Spiral striation absent or present. Aperture tilted up to 30° relative to the coiling axis of the spire, circular to elliptic, Peristome simple (because outer and inner peristome fused) or double; when simple spreading, often with a somewhat thickened lip; when double outer peristome slightly spreading beyond the inner or not, if so gradually narrowed towards the right side of the aperture, and there absent, outer peristome sometimes slightly widened along the upper side; inner peristome usually slightly protruding from the outer, spreading. Dimensions. Height of spire without tuba 1.7–2.1 mm; width 1.4–1.6 mm; ratio height/width 1.3–1.5; width including tuba 2.4–2.7 mm; umbilicus 0.30–0.40 mm wide; number of whorls 5 1/2–6 1/8, excluding the tuba; height and width aperture 0.6–0.7 mm.

Distribution in Sabah. Rare in W: Trus Madi range, Sinobang, Sapulut. Elevation range: 300–1100 m. In (disturbed) primary forest, mature coastal woodland, on limestone bedrock. Endemic to Sabah.

Variability. Variability occurs in the flat or slightly convex sides of the spire, in the presence/absence of spiral striation, and in the simple/double peristome. A similar variability occurs in *Plectostoma dormani*, from the same area.

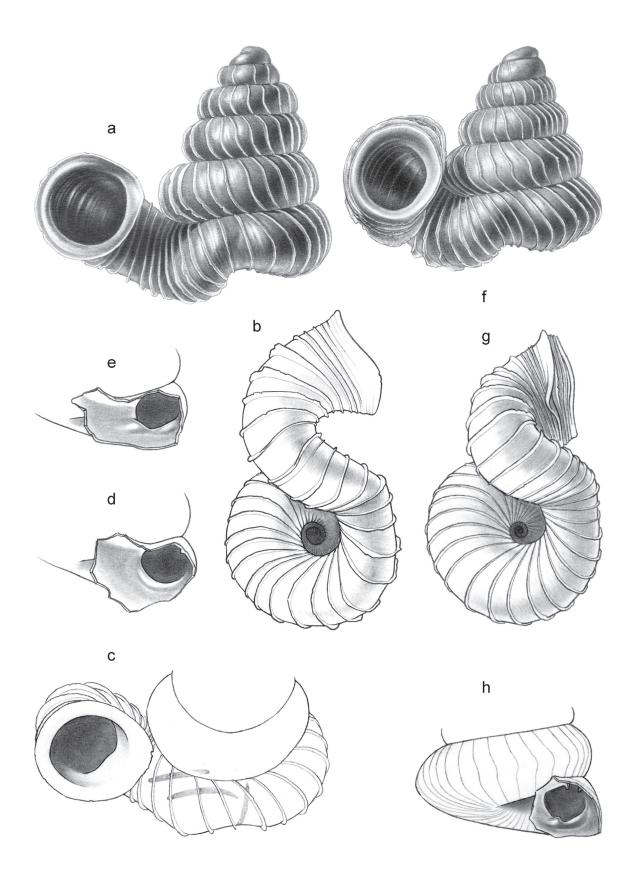


Fig. 68, a—e. *Plectostoma obliquedentatum* (Vermeulen, 1994), a. Frontal view, shell 2.2 mm high, b. Umbilical view, c. Oblique frontal view to show position of teeth in the constriction, d—e. Left lateral views with tuba removed to show inner surface of constriction; f—h. *Plectostoma simplex* (Fulton, 1901), f. Frontal view, shell 2.0 mm high, g. Umbilical view, h. Left lateral view with tuba removed to show inner surface constriction.

Plectostoma simplex (Fulton, 1901)

(fig. 68f-h, map 11f)

Opisthostoma simplex Fulton 1901: 243; Vermeulen 1994: 112; Schilthuizen et al. 2006: 1851; Clements et al. 2008: 2762. – Opisthostoma (Plectostoma) simplex (Fulton) Kobelt 1902: 417; Von Martens 1908: 258. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Differs from *Plectostoma obliquedentatum* by the outer peristome which develops into a slight wing along the upper side of the peristome, before abruptly narrowing to its right side. Also, *P. simplex* always has a parietalis, which is not oblique.

Description. Spire conical with slightly concave to slightly convex sides. Apex not oblique. Whorls convex; last whorl rounded to slightly angular. Constriction with 4 teeth: 1 parietalis; 1 longitudinal and 1 transverse palatalis; 1 columellaris which continues as a knob- to ridge-shaped transverse basalis. Tuba gradually narrowed towards the constriction, rounded below. Sculpture. Radial ribs on the spire rather closely placed to moderately spaced (4–5 ribs/0.5 mm on the penultimate whorl), sinuous or not, but those close to the tuba not sinuous; radial ribs on the tuba moderately spaced (3 ribs/0.5 mm half-way), slightly sinuous below. Spiral striation present, often inconspicuous. Aperture tilted up to 30° relative to the coiling axis of the spire, circular, elliptic or slightly angular. Peristome touching the spire or distant from it, double; outer peristome spreading beyond the inner, gradually to rather abruptly narrowed towards the right side of the aperture, and there absent, usually with a distinct, obtuse (rounded but not widely so) wing along the upper side, and sometimes with a similar but less conspicuous wing along the lower side; inner peristome moderately protruding from the outer, often with a few protruding lamellae on its outer surface, spreading. Dimensions. Height of spire without tuba 1.5–2.2 mm; width 1.2–1.6 mm; ratio height/width 1.2–1.5; width including tuba 2.0–2.5 mm; umbilicus 0.25–0.40 mm wide; number of whorls 5 1/8–6 3/8, excluding the tuba; height and width aperture 0.5–0.6 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Variability. Schilthuizen et al. (2006) include this in the *Plectostoma concinnum* species complex. *Plectostoma simplex* does not occur sympatrically with shells identified as *P. concinnum*, but morphological intermediates do occur in populations of both species.

Family **PUPINIDAE** L Pfeiffer, 1853

Diagnosis for the Sabah species. Shell dextral, small to large, ovoid to conical with (narrowly) obtuse apex. Constriction in the last whorl absent. A pore in the inner surface, close to the suture and to the aperture, is absent. Color white to corneous to dark red. Sculpture absent or weak. Aperture with or without a subangular lamella. Peristome thickened, spreading, interrupted by a deep sinus on the basal side or not. Umbilicus open or closed and covered by the peristome. Operculum corneous, circular, with many whorls; nucleus central.

Genus *Coptocheilus* Gould, 1862

(= Schistoloma Kobelt, 1902)

Diagnosis for the Sabah species. Shell opaque, ochre-brown to dark red-brown. Surface shiny, with weak sculpture. Umbilicus open, narrow. Shell height 23–29 mm.

Note. Bui & Páll-Gergely (2020) reinstate Coptocheilus instead of Schistoloma, because the latter is ill-founded replacement name.

Coptocheilus anostomus (Benson, 1852)

(fig. 69a-c, 70b, map 12a)

Kobelt & Von Möllendorff 1897a: 142; Bui & Páll-Gergely 2020: 449. – *Cyclostoma anostoma* Benson 1852: 269. – *Megalomastoma anostoma* (Benson) Pfeiffer 1854d: 89; 1858: 85; Von Martens 1867: 154; Issel 1874: 66; Tenison Woods 1888: 1072; Godwin-Austen 1889: 352. – *Schistoloma anostoma* (Benson) Kobelt 1902: 278. – Type from 'Borneo'.

Description. Shell large, rather solid, opaque, ochre-brown to dark red-brown. Surface shiny. Spire elongated-conical with somewhat convex sides, apex narrowly rounded. Whorls moderately convex, last whorl evenly rounded, but slightly more narrowly rounded below the periphery. Sculpture. Radial sculpture: Growth lines, locally with unevenly but narrowly spaced, inconspicuous, low, flat, rounded riblets. Spiral sculpture: An inconspicuous, shallow subsutural groove present in some shells, spiral sculpture otherwise absent, or locally with

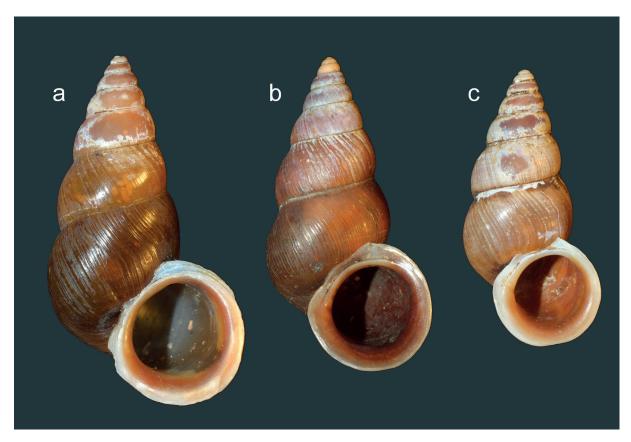


Fig. 69, a-c. *Coptocheilus anostomus* (Benson, 1852), frontal views; a. Shell 27 mm high; b. Shell 24 mm high; c. Shell 21.5 mm high.

traces of rather densely placed, very shallow grooves, mainly cutting into the crests of the radial sculpture, approx. absent below the periphery. Umbilicus open, very narrow. Dimensions. Height 23–29 mm; width 10.5–15.5 mm; ratio height/width 1.7–2.2; number of whorls 7 1/4–8; height aperture 8.5–12.0 mm; width aperture 8.8–11.0 mm.

Distribution in Sabah. Labuan only (old record). Elevation range: 0–100 m. Elsewhere in forest on limestone bedrock. Also in Sarawak. Distribution elsewhere: Malaysia (Peninsula); distribution uncertain because of unsettled taxonomy.

Note. The subsutural furrow in our description is the same as the 'double suture' in Bui & Páll-Gergely (2020).

Genus Pupina Vignard, 1829

Diagnosis for the Sabah species. Shell thin, translucent or transparent, white, pale yellow to brown-corneous. Surface glossy, without sculpture. Umbilicus closed, covered by the peristome. Shell height 6.2–8.1 mm.

Note. The parietal peristome extends over the entire shell as a thin, smooth glazing. This layer may peel off in weathered specimens, revealing a shell surface with a different sculpture.

Pupina hosei Godwin-Austen, 1889

(fig. 70a, 71, map 12a)

Godwin-Austen 1889: 351; Smith 1895: 124; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Marzuki et al. 2021: 36. – *Pupina (Tylotoechus) hosei* (Godwin-Austen) Kobelt & Von Möllendorff 1897a: 144; Kobelt 1902: 314; Von Martens 1908: 257. – Type from Malaysia, Sarawak, 'Busau Hills'.

Pupina c.f. artata auct. Saul 1967: 110.

Pupina sp. Schilthuizen & Rutjes 2001: 420; Foon et al. 2018: 96.

[Not Pupina artata Benson].

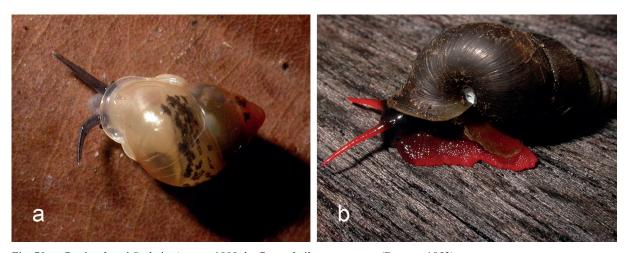


Fig. 70, a. Pupina hosei Godwin-Austen, 1889; b. Coptocheilus anostomus (Benson, 1852).

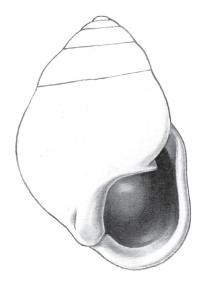


Fig. 71. *Pupina hosei* Godwin-Austen, 1889, frontal view, shell 6.2 mm high.

Description. Shell small, thin, translucent or transparent, white, pale yellow to brown-corneous. Surface glossy. Spire obliquely ovoid, apex narrowly rounded. Whorls moderately convex, last whorl evenly rounded. Sculpture. No sculpture present, but underneath the glossy, easily eroding top layer a fine radial sculpture consisting of densely placed riblets. Aperture drop-shaped, with a rather high parietal lamella which is placed so that a virtually circular aperture remains; this lamella reaching approx. 1/8 whorl into the spire. Peristome of paler color than the shell or white, somewhat thickened and distinctly spreading, single; in the basal corner with a deep furrow of which the edges (almost) touch, the upper edge the termination of a short columellar lamella. Umbilicus closed and entirely covered. Dimensions. Height 6.2-8.1 mm; width 4.1-5.9 mm; ratio height/width 1.3-1.7; number of whorls 4 7/8-5 3/8; height aperture 3.4-4.2 mm; width aperture 2.4-3.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2200 m. Primary forest and degraded woodland, most on limestone bedrock, but also on volcanic and granodiorite bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Malaysia (Peninsula), Thailand, Laos; see below.

Similar species elsewhere. Pupina siamensis Von Möllendorff, 1902 and *P. excisa* Von Möllendorff, 1902, from Laos, Thailand and Peninsular Malaysia are probably the same species. The latter appears slightly larger (height 8–9 mm) but is otherwise is not different.

Subclass: CAENOGASTROPODA Order: LITTORINIMORPHA

Family **ASSIMINEIDAE** H & A Adams, 1856

Diagnosis for the Sabah species. Shell dextral, very small, ovoid to conical with obtuse to almost acute apex. Constriction absent, or present in the last whorl. A pore in the inner surface, close to the suture and to the aperture or to the constriction, is absent. Color white to corneous or orange to dark (red-)brown. Sculpture approx. absent, or spiral and/or radial sculpture present. Aperture without teeth. Peristome usually not thickened (thickened in Anaglyphula), not spreading. Umbilicus closed or open, usually narrow. Operculum corneous, obliquely elliptic or ovate, without a peg on the inside, with few whorls; nucleus distinctly excentric.

Notes. 1. Family description adapted from Fukuda & Ponder (2003) and Miranda et al. (2014).

2. The genera are arranged according to environmental preference: First the fully terrestrial genera, then the amphibious (freshwater or marine) species.

The fully terrestrial species

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Spire with a slight constriction about 1/2 whorl back of the aperture, consisting of a circular rim inside, which shines through as a thin, white line outside

 Genus *Anaglyphula*
- 1 Spire without constriction

Genus Acmella

Genus Acmella W T Blanford, 1869

Diagnosis for the Sabah species. Spire without constriction. Umbilicus open, often with a slight thread starting on the columellar side of the peristome, close to the columellar corner, and spiraling (steeply) upwards. Peristome usually not or hardly thickened (except sometimes in gerontic shells).

Notes. 1. In several species long and slender shells occur next to shorter and wider ones. The umbilical thread is sometimes inconspicuous and difficult to see, a mere strip of somewhat rougher sculpture that betrays its presence by the dirt that accumulates around it.

2. The species with predominant radial sculpture most resemble the type species of *Acmella*, see Das et al. (in press).

KEY TO THE GROUPS

1 - Radial sculpture predominant

Group 1

Spiral sculpture predominant, or radial and spiral sculpture about equally strong, or virtually no sculpture present

Group 2

Group 1

Acmella cyrtoglyphe Vermeulen, Liew & Schilthuizen, 2015

(fig. 72a–d, map 12b)

Vermeulen et al. 2015: 7; Marzuki et al. 2021: 37. – Type from Malaysia, Sabah, Interior Prov., Sapulut valley, Gua Sanaron.

Acmella cyrtoglyphe, unavailable name, Clements et al. 2008: 2761.

Description. Shell minute, thin, somewhat translucent, white. Surface shiny. Spire conical with approx straight sides, apex obtuse. Whorls convex, sometimes slightly shouldered. Sculpture. Radial sculpture predominant: Densely placed to moderately spaced, evenly spaced, prosocline riblets which are distinctly sinuous around the periphery, and which below the periphery are about as strong as above or finer, some bifurcating from the periphery downwards, and with few to many finer riblets in between. Spiral threads usually present, visible in between the radial riblets, inconspicuous to rather distinct, (rather) densely placed at regular intervals. Aperture approx. obliquely elliptic in outline, obtuse above, with a straight parietal side, transition from parietal to basal side rounded to obtusely angular. Peristome not thickened. Umbilicus open, (rather) wide. Dimensions. Height 1.00–1.50 mm; width 0.85–1.10 mm; ratio height/width 1.10–1.36; number of whorls 4 1/8–5 7/8; height aperture 0.35–0.50 mm; width aperture 0.37–0.50 mm.

Distribution in Sabah. Scattered localities in E and SW. Elevation range: 0–700 m. In primary and secondary forest on limestone bedrock, Also in Sarawak, Kalimantan. Endemic to Borneo.

Similar species elsewhere. Shares the prominent, prosocline radial sculpture with Acmella roepstoffiana G Nevill, 1878 (India, Nicobar islands), differs by the more convex whorls and the wider umbilicus, which is not at all covered by the peristome.

Variability. The material is variable in two characters: The ratio height/width varies (and with it the width of the umbilicus); as well as the spacing of the radial ribs above the periphery. Specimens with moderately spaced radial ribs above the periphery have the radial ribs bifurcating more frequently below the periphery. However, we find it impossible to distinguish separate units.

Acmella umbilicata Vermeulen, Liew & Schilthuizen, 2015

(fig. 72e–g, map 12c)

Vermeulen et al. 2015: 9. – Type from Malaysia, Sabah, Interior Prov., Pinangah river valley, Batu Urun (= Sinobang hill).

Acmella umbilicata, unavailable name, Clements et al. 2008: 2761.

Cross diagnosis. Differs from Acmella cyrtoglyphe by the almost orthocline radial ribs.

Description. Shell minute, thin, somewhat translucent, white. Surface shiny. Spire conical with straight or slightly concave sides, apex obtuse. Whorls convex, sometimes slightly shouldered. Sculpture. Radial sculpture predominant: Densely placed and evenly spaced, almost orthocline riblets which are about straight with only locally a few slightly sinuous around the periphery, and which below the periphery are about as strong and as numerous as above, rarely bifurcating. Spiral threads inconspicuous or almost absent. Aperture approx. obliquely elliptic in outline, obtuse above, with a straight parietal side, transition from parietal to basal side rounded to obtusely angular. Peristome not thickened. Umbilicus open, very wide. Dimensions. Height 1.15–1.50 mm; width 0.95–1.15 mm; ratio height/width 1.00–1.37; number of whorls 4 1/8–5; height aperture 0.45–0.55 mm; width aperture 0.45–0.50 mm.

Distribution in Sabah. Sinobang and Sapulut only. Elevation range: 300–500 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Variability. Just as in Acmella cyrtoglyphe, we observe variability in the ratio height/width of the shell, and with it in the width of the umbilicus.

Group 2

Acmella nana Vermeulen, Liew & Schilthuizen, 2015

(fig. 73a-b, map 12d)

Vermeulen et al. 2015: 14; Marzuki et al. 2021: 39. – Type from Malaysia, Sarawak, 4th Division, Niah Caves, S side of limestone area, W side of quarry, soil-filled crevice opened in quarry. *Acmella nana*, unavailable name, Clements et al. 2008: 2761.

Cross diagnosis. Like *Acmella ovoidea* but smaller, with a narrower spire than juvenile *A. ovoidea* of the same size. It also has coarser spiral sculpture.

Description. Shell minute (one of the smallest Bornean snail species), thin, translucent, white. Surface shiny. Spire conical with almost flat to distinctly convex sides, apex broadly obtuse. Whorls moderately convex, sometimes slightly shouldered. Sculpture. Radial sculpture subordinate to the spiral sculpture: Scattered, inconspicuous growth lines only, grading into somewhat coarser riblets at uneven intervals. Spiral sculpture: Rather conspicuous, densely placed and evenly spaced, fine, low and wide threads with only very narrow grooves in between. Aperture obliquely ovate in outline, obtuse above, with a slightly concave to slightly convex parietal side, transition from parietal to basal side rounded to obtusely angular. Peristome not thickened. Umbilicus open, narrow. Dimensions. Height 0.60–0.79 mm; width 0.50–0.60 mm; ratio height/width 1.00–1.35; number of whorls 2 7/8–3 7/8; height aperture 0.30–0.37 mm; width aperture 0.26–0.30 mm.

Distribution in Sabah. Widespread, rare: Sinobang, Sapulut, lower Kinabatangan. Elevation range: 0–500 m. In (disturbed) primary forest on limestone bedrock. Also in Sarawak and Kalimantan. Endemic to Borneo.

Similar species elsewhere. Resembles Acmella caelata Vermeulen & Junau, 2007 (Sarawak). This species is consistently wider (c. 0.7 mm in A. caelata, 0.50–0.60 mm in A. nana). If specimens with the same number of whorls are compared, the whorls of A. caelata are less depressed (at 3 1/8–3 3/8 whorl A. caelata is 0.80–0.95 mm high, A. nana only 0.60–0.75 mm).

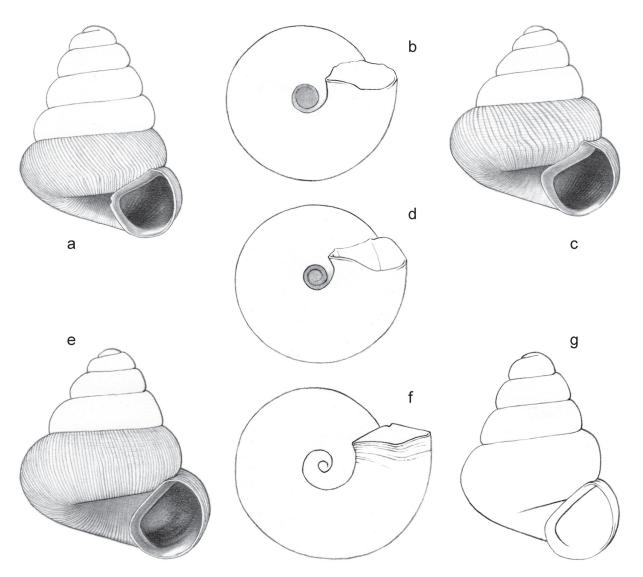


Fig. 72, a–d. *Acmella cyrtoglyphe* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.4 mm high, b. Umbilical view, c. Frontal view, shell 1.1 mm high, d. Umbilical view; e–g. *Acmella umbilicata* Vermeulen, Liew & Schilthuizen, 2015, e. Frontal view, shell 1.3 mm high, f. Umbilical view, g. Frontal view, shell 1.3 mm high.

Acmella ovoidea Vermeulen, Liew & Schilthuizen, 2015

(fig. 73c–f, map 12e)

Vermeulen et al. 2015: 12; Marzuki et al. 2021: 41. – Type from Malaysia, Sabah, Interior Prov., Pinangah river valley, Batu Urun (= Sinobang hill).

Acmella ovoidea, unavailable name, Clements et al. 2008: 2761.

Acmella sp. 'bor-01 [V 7980]': Schilthuizen & Vermeulen 2003a: 95.

Acmella minutissima auct. Schilthuizen et al. 2013: Online supplementary data.

[Not Anaglyphula minutissima Maassen].

Cross diagnosis. Among Sabah *Acmella* species characterized by the approx. ovoid outline of the shell in combination with the predominant, very fine, spiral sculpture.

Description. Shell minute, rather thin, translucent, white. Surface shiny. Spire conical with slightly convex sides to ovoid, apex (broadly) obtuse. Whorls slightly to moderately convex, sometimes slightly shouldered. Sculpture. Radial sculpture subordinate to the spiral sculpture: Scattered, inconspicuous growth lines only, in some shells locally grading into slight, densely placed and evenly spaced riblets on the crests of the spiral threads.

Subclass: CAENOGASTROPODA Order: LITTORINIMORPHA

Spiral sculpture: Densely placed and evenly spaced, very fine, low and wide threads with only narrow grooves in between. Aperture obliquely ovate in outline, acute to slightly obtuse above, with a concave to slightly convex parietal side, transition from parietal to basal side rounded. Peristome not thickened. Umbilicus open, narrow. Dimensions. Height 0.85–1.35 mm; width 0.80–1.00 mm; ratio height/width 1.00–1.35; number of whorls 3 1/2–5; height aperture 0.40–0.55 mm; width aperture 0.40–0.50 mm.

Distribution in Sabah. Scattered localities in E, but common in lower Kinabatangan; rare in SW: Pun Batu, Bukit Melikop, Sinobang, Sapulut. Elevation range: 0–700 m. In primary and secondary forest on limestone bedrock. Also in Sarawak, Kalimantan Timur. Endemic to Borneo.

Similar species elsewhere. Acmella minutissima (Maassen, 2000) (Anaglyphula minutissima Maassen, 2000, from Indonesia, Sumatra), differs by having a conical shell and narrower spiral threads, with dense radial riblets visible in the furrows in between.

Variability. The ratio height/width is highly variable, and the umbilicus may be wider than in the illustrated shell.

Acmella polita Von Möllendorff, 1887

(fig. 73g-h, map 12f)

Von Möllendorff 1887a: 301; Schilthuizen & Vermeulen 2003a: 95; Clements et al. 2008: 2761; Vermeulen et al. 2015: 10; Phung et al. 2017: 56. – Type from Philippines, Luzon, Montalban near Manilla.

Cross diagnosis. The largest Acmella species in Sabah.

Description. Shell very small, rather thick, hardly translucent, white. Surface dull or somewhat shiny. Spire conical with approx. straight or slightly convex sides, apex obtuse. Whorls moderately convex. Sculpture. Radial sculpture: Scattered, inconspicuous growth lines only, at uneven intervals, locally often very fine, dense riblets. Spiral sculpture (almost) absent, or locally a very fine, dense spiral striation, just visible at 40x magnification. Aperture obliquely elliptic to broadly ovate in outline, acute above, with a straight or slightly curved parietal side, transition from parietal to basal side rounded to obtusely angular. Peristome not thickened. Umbilicus open, (rather) narrow. Dimensions. Height 1.95–4.50 mm; width 1.4–3.0 mm; ratio height/width 1.18–1.50; number of whorls 4 3/4–6 1/2; height aperture 0.85–2.00 mm; width aperture 0.90–1.70 mm.

Distribution in Sabah. Scattered localities in E, but common in lower Kinabatangan; rare in SW: Labuan, Pun Batu, Sapulut. Elevation range: 0–500 m. In primary and secondary forest on limestone bedrock, often in caves. Also in Kalimantan (E part). Distribution elsewhere: Philippines.

Acmella striata Vermeulen, Liew & Schilthuizen, 2015

(fig. 73i-j, map 13a)

Vermeulen et al. 2015: 16; Phung et al. 2017: 56. – Type from Malaysia, Sabah, Kudat Prov., Balambangan island, S end, Batu Sireh.

Acmella striata, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

Cross diagnosis. Characterized among Sabah *Acmella* by the elongated spire with distinctly convex whorls, and wavy spiral sculpture on the teleoconch.

Description. Shell minute, rather thin, slightly translucent, (dark) corneous to white. Surface shiny. Spire conical with approx. straight sides, apex somewhat narrowly obtuse. Whorls convex, often somewhat shouldered. Sculpture. Radial sculpture subordinate to the spiral sculpture: Growth lines, grading into widely and unevenly spaced riblets locally. Spiral sculpture: Densely placed to moderately spaced, thin, narrow, very fine, distinctly wavy spiral threads which are occasionally interrupted or bifurcated, which have shallow and wide spaces in between and which run either approx. parallel to the suture or run slightly obliquely downwards in the direction of the aperture. Aperture approx. elliptic in outline, obtuse above, with a slightly convex parietal side, transition from parietal to basal side rounded. Peristome not thickened. Umbilicus open, narrow. Dimensions. Height 1.40–1.80 mm; width 1.05–1.25 mm; ratio height/width 1.33–1.44; number of whorls 4 1/8–5 1/4; height aperture 0.50–0.70 mm; width aperture 0.55–0.65 mm.

Distribution in Sabah. Scattered localities in S and E; elsewhere Mantanani islands, Balambangan island only. Elevation range: 0–600 m. In primary forest, primary coastal woodland and secondary vegetation on limestone bedrock, also found on sandstone/shale and volcanic bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Indonesia (Ambon, Ceram, Tanimbar islands).

Similar species elsewhere. Resembles Acmella sutteri Van Benthem Jutting, 1958, from Sumba. Acmella striata differs by the parietal side of the aperture, which is attached to the previous whorl over slightly more than half the distance between the periphery and the umbilicus of the latter. In A. sutteri it is only attached to the previous whorl over a very short distance near the upper corner.

Variability. Shells from Mantanani and Balambangan islands are relatively large and of dark color. Similar

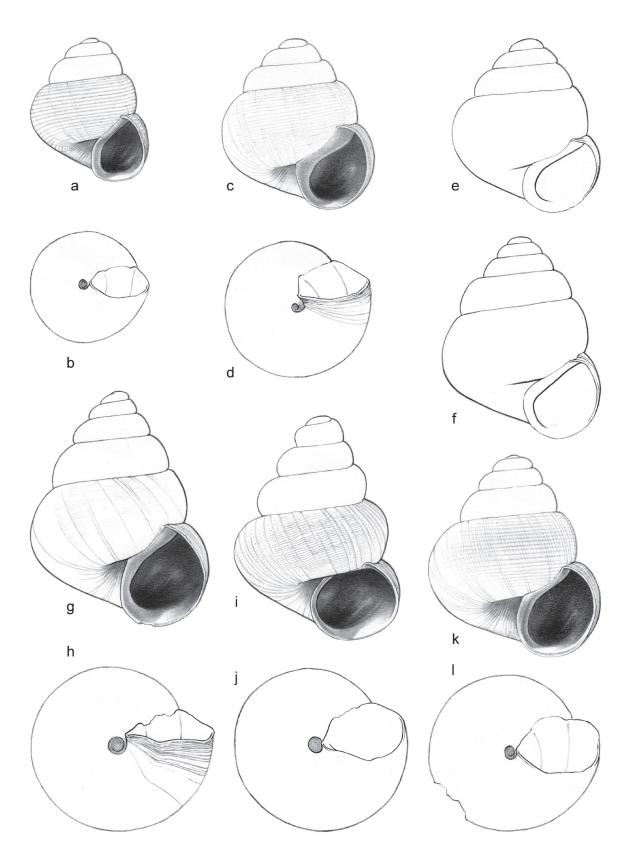


Fig. 73, a–b. *Acmella nana* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 0.7 mm high, b. Umbilical view; c–f. *Acmella ovoidea* Vermeulen, Liew & Schilthuizen, 2015, c. Frontal view, shell 1.2 mm high, d. Umbilical view; e. Frontal view, shell 1.15 mm high, f. Frontal view, shell 1.35 mm high; g–h. *Acmella polita* Von Möllendorff, 1887, g. Frontal view, shell 2.3 mm high, h. Umbilical view; i–j. *Acmella striata* Vermeulen, Liew & Schilthuizen, 2015, i. Frontal view, shell 1.6 mm high, j. Umbilical view; k–l. *Acmella subcancellata* Vermeulen, Liew & Schilthuizen, 2015, k. Frontal view, shell 1.4 mm high, l. Umbilical view.

shells are found locally in the Kinabatangan river valley, but towards the W populations grade into a smaller form with white shells, as is found in Gunung Mulu N.P., Sarawak. A sample from Kalimantan contains medium-sized and white shells. Most Sabah specimens have a slightly oblique spiral striation. In Sarawak shells with a spiral striation parallel to the suture predominate in most localities.

Acmella subcancellata Vermeulen, Liew & Schilthuizen, 2015

(fig. 73k–l, map 13b)

Vermeulen et al. 2015: 14. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong c. 50 km WSW of Lahad Datu.

Cross diagnosis. Like Acmella ovoidea; differs by its conical shell and more prominent sculpture.

Description. Shell minute, rather thin, somewhat translucent, white. Surface shiny. Spire conical with straight to slightly convex sides, apex somewhat narrowly obtuse. Whorls (moderately) convex, sometimes slightly shouldered. Sculpture. Radial sculpture subordinate to the spiral sculpture: Scattered, inconspicuous growth lines, grading into inconspicuous, rather densely placed and evenly spaced riblets on the crests of the spiral threads. Spiral sculpture: Densely placed and evenly spaced, very fine, low and wide threads with only very narrow spaces in between. Aperture obliquely ovate in outline, acute above, with a slightly concave to approx. straight parietal side, transition from parietal to basal side rounded. Peristome not thickened. Umbilicus open, narrow. Dimensions. Height 1.19–1.30 mm; width 0.95–1.10 mm; ratio height/width 1.11–1.26; number of whorls 4 1/8–4 1/2; height aperture 0.58–0.69 mm; width aperture 0.49–0.59 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 100–200 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. The general shell shape resembles Acmella minutissima (Maassen, 2000) (Anaglyphula minutissima Maassen, 2000), from Indonesia, Sumatra. Acmella subcancellata is larger (shell height 1.19–1.30 mm, width 0.95–1.10 mm, versus c. 0.8 mm and 0.65 mm respectively), and differs by its teleochonch sculpture of much wider spiral threads, leaving only narrow spaces in between.

Genus Anaglyphula B Rensch, 1932

Diagnosis for the Sabah species. Spire with a slight constriction about 1/2 whorl back of the aperture, consisting of a circular rim on the inner surface, on the outside this rim shines through as a thin, white line. Umbilicus open, without thread. Peristome thickened.

Notes. If the constriction is not visible because the shell has turned opaque, the thickened peristome may serve to distinguish the genus from *Acmella*.

Anaglyphula sauroderma Vermeulen, Liew & Schilthuizen, 2015

(fig. 74a-b, map 13c)

Vermeulen et al. 2015: 18; Marzuki et al. 2021: 41. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Batu Baturong c. 50 km WSW of Lahad Datu.

Cross diagnosis. The sculpture uniquely identifies the species among the Sabah snail fauna.

Description. Shell minute, rather thick, about opaque, pale corneous. Surface shiny. Spire conical with approx. straight or slightly concave sides, apex somewhat narrowly obtuse. Whorls moderately convex. Sculpture consisting of radial ribs intersecting with about equally strong spiral threads, creating a pattern of rounded shallow depressions on the shell surface; locally this pattern is distorted, and around the periphery and below the suture the depressions line up parallel to the growth lines; close to the aperture radial riblets and growth lines predominate. Aperture widely and obliquely ovate in outline, acute above, with a slightly concave parietal side, transition from parietal to basal side obtusely angular. Peristome thickened, with a slight lip on the inner side. Umbilicus open, narrow. Dimensions. Height c. 1.75 mm; width c. 1.45 mm; ratio height/width c. 1.25; number of whorls c. 5; height aperture c. 0.80 mm; width aperture c. 0.70 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 100–200 m. In primary forest on limestone bedrock. Also in Sarawak, Kalimantan Timur. Endemic to Borneo.

Similar species elsewhere. Anaglyphula sauroderma shares the uneven cancellate sculpture with shallow pits with A. cancellata B Rensch, 1932 (Indonesia, Flores). It differs by a more elongated spire (distinctly higher than wide) and evenly rounded whorls.

The amphibious species (freshwater, brackish environments, and maritime mudflats)

Notes. 1. With six genera each with a single species we give diagnostic character combinations for the species

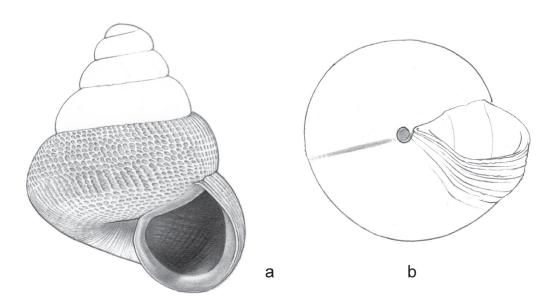


Fig. 74, a-b. *Anaglyphula sauroderma* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.8 mm high, b. Umbilical view, position of constriction indicated in grey shading.

rather than for the genera. Diagnoses for the genera can be found in Fukuda & Ponder (2003), with additional information on *Taiwanassiminea* in Fukuda et al. (2015).

- 2. We have few in situ records of amphibian Assimineidae, except for *Optediceros breviculum*. All other species are mainly known from a few, usually bleached shells found in near-coastal but fully terrestrial soil samples, or in beach drift samples. The latter are often juveniles.
- 3. In species from brackish and maritime environments, juveniles often more distinctly display characters of the apical part of the shell and of the umbilical area. The apex is often eroded in adults and features in the umbilical area tend either to become obsolete, or so prominent that they overgrow other features, for instance an umbilical thread and a thickened peristome covering an open umbilicus.
- 4. More species may occur on Sabah's coast. For identification we advise Abbott (1958), Brandt (1974), Van Benthem Jutting (1956), and Zilch (1967).

Genus Assiminea Fleming, 1828

Note. Amphibious snails in brackish and maritime environments.

Assiminea nitida (Pease, 1865)

(fig. 75e–f, map 13d)

Boettger 1887: 211; Zilch 1967: 69; Abbott 1958: 254; Brandt 1974: 148; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data. – *Hydrocena nitida* Pease 1865 (1864): 674. – *Realia* (?) *nitida* (L Pfeiffer) Pfeiffer 1876: 212. – *Syncera nitida* (Pease) Abbott 1949: 272; Van Benthem Jutting 1956: 355; 1959: 91. – Type from 'Huaheine, Pacific islands'.

Cross diagnosis. Resembles *Taiwanassiminea bedaliensis*, differs by the more conical spire, with at most slightly convex sides, and by the less convex whorls. Also, *A. nitida* is uniformly brown, not banded. *Optediceros breviculum* and *Ovassiminea obtusa* have a wider shell (ratio height/width 1.21–1.38, versus 1.45–1.70); the first is also distinctly larger.

Description. Shell very small, thick, opaque, (pale) ochre to red-brown. Surface shiny. Spire conical with approx. straight or slightly convex sides, apex acute (but often eroded). Whorls almost flat to slightly convex, the last slightly flattened above the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Scattered, inconspicuous growth lines. Spiral sculpture: 1 fine subsutural groove, next to this locally very fine and inconspicuous (just visible at 40x magnification), dense striation. Aperture obliquely ovate in outline, acute above, approx. straight on the parietal side, transition from parietal to basal side narrowly rounded, basal side rounded. Peristome not thickened. Umbilicus closed, covered by the slightly widened peristome. Dimensions. Height up to 3.5 mm;

Subclass: CAENOGASTROPODA Order: LITTORINIMORPHA

width up to 2.1 mm; ratio height/width 1.45–1.70; number of whorls up to 7; height aperture up to 1.35 mm; width aperture up to 1.0 mm.

Distribution in Sabah. Recorded from Balambangan and Banggi islands only, probably more widespread. Elevation: 0 m. On maritime mudflats, silty beaches, in mangrove woodland. Living on stones, wood, and dead organic matter. Distribution elsewhere: Coasts of Indian and Pacific Ocean, N to China.

Note. Description based on fully adult specimens. Juveniles are wider-conical, and with more distinctly convex whorls. The spire, however, is always narrower than in other Sabah amphibious assimineids.

Genus Optediceros Leith, 1853

Note. Amphibious snails in maritime environments.

Optediceros breviculum (L Pfeiffer, 1855)

(fig. 75a-b, 76a, map 13e)

Fukuda & Ponder 2003: 2018. – *Hydrocena brevicula* Pfeiffer 1855 (1854c): 306. – *Realia* (?) *brevicula* (L Pfeiffer) Pfeiffer 1876: 210. – *Assiminea brevicula* (L Pfeiffer) Nevill 1881: 159; Von Martens 1908: 271; Abbott 1958: 238; Zilch 1967: 67. – *Syncera brevicula* (L Pfeiffer) Van Benthem Jutting 1956: 358; 1859: 90. – *Assiminea (Sphaerassiminea) brevicula* (L Pfeiffer) Brandt 1974: 145. – Type from Singapore.

Assiminea miniata Von Martens 1866: 204. – Assiminea brevicula (L Pfeiffer) var. miniata (E Von Martens) Von Martens 1897: 214. – Assiminea brevicula (L Pfeiffer) f. miniata (E Von Martens) Van Benthem Jutting 1956: 359; 1959: 90; Solem 1964: 21. – Type from Singapore.

Assiminea rubella Blanford 1867a: 384; Issel 1874: 450. - Type from Myanmar, 'Irawaddy Delta'.

Cross diagnosis. Characterized among Sabah amphibious assimineids from maritime or brackish environments by its size (shell up to 7 mm high at 6 3/8 whorls, versus 3.4–3.9 mm). *Solenomphala scalaris* approaches *Optediceros breviculum* in size (shell up to 5.8 mm high) but differs by its spiral sculpture. Contrary to *Optediceros*, it is from freshwater environments.

Description. Shell small, thick, opaque, (pale) brown to (orange-)red. Surface shiny. Spire obliquely ellipsoid to ovoid, apex acute (but often eroded). Whorls almost flat to slightly convex, the last evenly rounded. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Scattered, inconspicuous growth lines. Spiral sculpture: 1–2 fine, widely spaced subsutural grooves, next to these locally very fine and inconspicuous (just visible at 40x magnification), dense striation. Aperture obliquely drop-shaped in outline, acute above, concave on the parietal side, transition from parietal to basal side rounded, basal side somewhat narrowly rounded. Peristome not thickened. Umbilicus rimate or closed, covered by the slightly widened peristome. Dimensions. Height up to 7.0 mm; width up to 5.4 mm; ratio height/width 1.27–1.38; number of whorls up to 6 3/8; height aperture up to 4.4 mm; width aperture up to 3.5 mm.

Distribution in Sabah. In coastal areas and on the islands: three records but undoubtedly more widespread. Elevation: 0 m. On maritime mudflats, silty beaches, in mangrove woodland, Nipa swamp. Living on mud, wood, fallen leaves etc. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: S and E Asia, SE-wards to Philippines, Indonesia (Java).

Genus Ovassiminea Thiele, 1927

Note. Amphibious snails in brackish environments.

Ovassiminea obtusa Wattebled, 1886

(fig. 76b-d, map 13e)

Hallan et al. 2015: 266. – *Assiminea obtusa* Wattebled 1886: 65. – *Assiminea (Ovassiminea) obtusa* (Wattebled) Brandt 1974: 146. – Type from Vietnam.

Cross diagnosis. Resembles Optediceros breviculum but is smaller and with more convex whorls.

Description. Shell very small, thick, opaque, pale yellow-corneous to pale brown-corneous. Surface (slightly) shiny. Spire ovoid, apex subacute (but often eroded). Whorls moderately convex, the last evenly rounded or slightly flattened above the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Scattered, inconspicuous growth lines. Spiral sculpture: Often an inconspicuous, very fine (just visible at 40x magnification), dense striation on the first whorl, other whorls usually without spiral striation, or locally with a few traces of a stri-

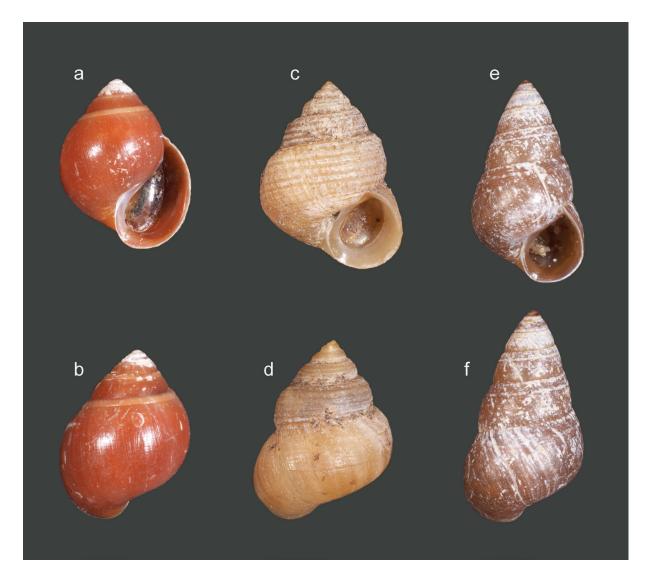


Fig. 75, a-b. *Optediceros breviculum* (L Pfeiffer, 1855), a. Frontal view, shell 4.9 mm high, b. Back view; c-d. *Sculptas-siminea microsculpta* (Nevill, 1880), c. Frontal view, shell 3.0 mm high, d. Back view; e-f. *Assiminea nitida* (Pease, 1865), e. Frontal view, shell 3.7 mm high, f. Back view.

ation like on the first whorl, last whorl usually with a fine thread on the periphery of the umbilical impression and a similar thread in the umbilicus, starting at the columellar peristome; a fine spiral striation is sometimes present in between these threads. Aperture obliquely ovate in outline, obtuse to acute above, approx. straight on the parietal side, transition from parietal to basal side somewhat narrowly rounded, basal side rounded. Peristome somewhat thickened on the parietal side. Umbilicus open, narrow, circular, in fully adult shells often rimate or closed, covered by the slightly widened peristome. Dimensions. Height up to 3.9 mm; width up to 2.9 mm; ratio height/width 1.21-1.33; number of whorls up to 5.3/4; height aperture up to 2.1 mm; width aperture up to 1.7 mm.

Distribution in Sabah. Recorded from Banggi island only, probably more widespread. Elevation: 0 m. Only known from juveniles in beach drift material. Elsewhere reported from lagoons and estuaries. Also in Brunei, Kalimantan. Distribution elsewhere: Thailand, Vietnam.

Similar species elsewhere. Assiminea borneensis (Issel, 1874) is similar but has a more distinct spiral striation. Variability. In fully adult specimens, the thread from the columellar peristome into the umbilicus lies very close to the edge of the columellar peristome or is even fused to it.

Genus Sculptassiminea Thiele, 1927

Note. Amphibious snails in brackish and maritime environments.

Sculptassiminea microsculpta (Nevill, 1880)

(fig. 75c–d, map 13f)

Fukuda & Ponder 2003: 2016. – *Assiminea microsculpta* Nevill 1880: 165. – *Syncera microsculpta* (Nevill) Van Benthem Jutting 1956: 361; 1959: 91. – *Assiminea (Sculptassiminea) microsculpta* (Nevill) Brandt 1974: 142. – Type from India, 'Fort Canning'.

Cross diagnosis. Identified among Sabah amphibian Assimineidae by the distinct sculpture on the last whorl, which includes distinct spiral threads from suture to base. Other Sabah amphibian Assimineidae either have no spiral sculpture on the last whorl, or 1–2 inconspicuous subsutural spiral threads or grooves and/or some very fine and inconspicuous spiral striation.

Description. Shell very small, thick, opaque, white to pale yellow-brown, last whorl with or without a wide, vaguely outlined, slightly darker brown spiral band above the periphery, and sometimes a second below. Surface dull or somewhat shiny. Spire ovoid(-conical), apex acute (but often eroded). Whorls slightly to moderately convex, the last evenly rounded or slightly flattened above the periphery. Sculpture. Protoconch with c. 7 fine, thin spiral threads. Teleoconch. Radial sculpture predominant or sometimes subordinate: Inconspicuous to distinct, (rather) densely placed, evenly spaced, low and rather flat ribs. Spiral sculpture: 14–16 widely spaced, fine to rather coarse, low, narrow to rather wide threads, when subordinate creating a cancellate sculpture together with the radial ribs. Aperture obliquely ovate in outline, obtuse to acute above, approx. straight on the parietal side, evenly rounded below or somewhat more narrowly rounded at the transition from parietal to basal side. Peristome not thickened. Umbilicus rimate, or open, very narrow. Dimensions. Height up to 3.4 mm; width up to 2.2 mm; ratio height/width 1.38–1.60; number of whorls up to 6 1/8; height aperture up to 1.4 mm; width aperture up to 1.4 mm.

Distribution in Sabah. Recorded from Labuan only, probably more widespread. Elevation: 0 m. On maritime mudflats, silty beaches, in mangrove woodland. Living on dead wood. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: S and E Asia, SE-wards to Philippines, Indonesia (Java).

Variability. In the illustrated specimen the spiral threads are predominant, and the radial sculpture is rather inconspicuous. In most other specimens the spiral sculpture is slightly subordinate, creating a cancellate sculpture together with the radial ribs.

Genus Solenomphala Heude, 1882

Note. Amphibious snails in freshwater environments.

Solenomphala scalaris (Heude, 1882)

(fig. 76e–f, map 13f)

Marzuki et al. 2021: 41. – Assiminea (Solenomphala) scalaris Heude 1882 (1882–1890): 83. – Cyclotropis scalaris (Heude) Tan et al. 2012: 68. – Type from China, Shanghai.

Cross diagnosis. Characterized among Sabah amphibious Assimineidae by the presence of low spiral threads over the entire shell. This sculpture is fine and inconspicuous, but nevertheless coarser and more continuous than any spiral striation present in species of the genera mentioned, *Assiminea microsculpta* excepted.

Description. Shell small, rather thick, approx. opaque, (pale) corneous to pale orange-brown, sometimes with an almost white umbilical region. Surface somewhat shiny. Spire ovoid-conical, apex acute. Whorls slightly convex, the last evenly rounded or slightly flattened above the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Scattered, inconspicuous growth lines, sometimes slightly raised at uneven intervals. Spiral sculpture: Rather densely placed, inconspicuous, flat, wide spiral threads, often 1 out of each 2–6 slightly more conspicuous and sometimes the ones in between almost absent, periphery of the umbilical impression with an inconspicuous, thin, low thread, and often a similar thread in the umbilicus, starting at the columellar peristome. Aperture obliquely ovate in outline, acute above, approx. straight or slightly concave on the parietal side, transition from parietal to basal side somewhat narrowly rounded, basal side rounded. Peristome thin on the parietal side, not thickened elsewhere. Umbilicus narrow. Dimensions. Height up to 5.8 mm; width up to 3.8 mm; ratio height/width 1.4–1.5; number of whorls up to 6 1/2; height aperture up to 2.8 mm; width aperture up to 2.0 mm.

Distribution in Sabah. Kota Kinabalu area only. Elevation range: 0–100 m. Found in concrete water container in urban area. Living amphibiously, just above the waterline, on the stone surface. Also in Sarawak. Distribution elsewhere: China, Singapore.

Similar species elsewhere. Several somewhat similar, but little-known species have been described from Borneo: Omphalotropis glabrata (L Pfeiffer, 1855) lacks the spiral sculpture; Omphalotropis radiata (L Pfeiffer, 1855) is angular at the periphery, white, and diaphanous; Assiminea cornea (Leith, 1853) lacks the spiral sculpture and has a 'subperforate' shell.

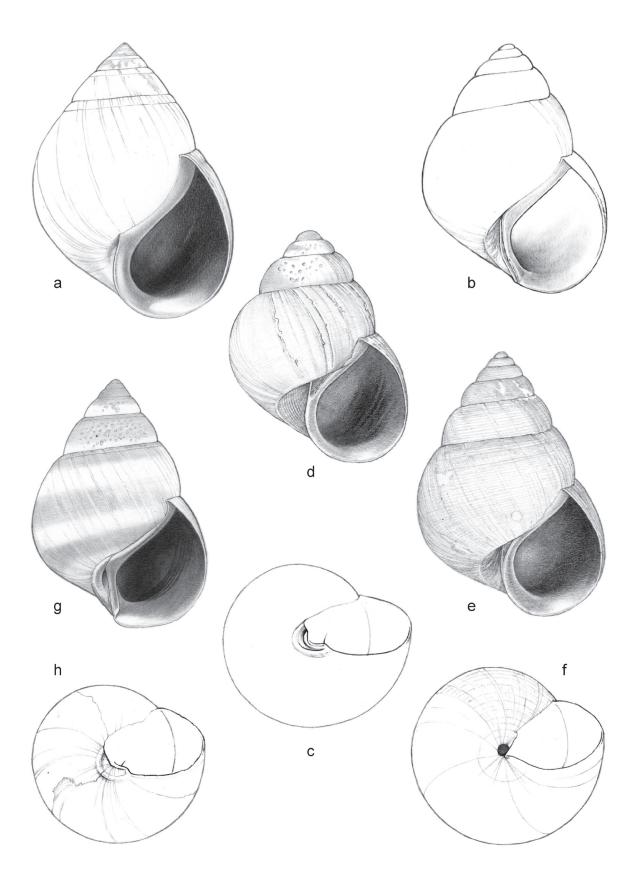


Fig. 76, a. *Optediceros breviculum* (L Pfeiffer, 1855), frontal view, shell 5.8 mm high; b–d. *Ovassiminea obtusa* Wattebled, 1886, b. Frontal view, shell 4.0 mm high, c. Umbilical view, d. Frontal view, shell 2.8 mm high; e–f. *Solenomphala scalaris* (Heude, 1882), e. Frontal view, shell 5 mm high, f. Umbilical view; g–h. *Taiwanassiminea bedaliensis* (B Rensch, 1934), g. Frontal view, shell 3.2 mm high, h. Umbilical view.

Genus Taiwanassiminea Kuroda & Habe, 1950

Note. Amphibious snails in freshwater and brackish environments.

Taiwanassiminea bedaliensis (B Rensch, 1934)

(fig. 76g-h, map 14a)

Fukuda et al. 2014 (2015): 27. – Assiminea bedaliensis Rensch 1934a: 226. – Syncera bedaliensis (B Rensch) Van Benthem Jutting 1956: 350. – Cyclotropis bedaliensis (B Rensch) Brandt 1974: 157. – Type from Indonesia, Java.

Cross diagnosis. Resembles *Assiminea nitida*, differs by the ovoid-conical spire, with distinctly convex sides, and by the more distinctly convex whorls. Also, the shells usually have color bands. Differs from *Solenomphala scalaris* by an absence of spiral striation apart from the subsutural groove.

Description. Shell very small, thick, opaque, almost white to pale yellow-brown, last whorl usually with a wide, vaguely outlined, slightly darker brown spiral band just above the periphery, and a second band lower down below the periphery. Surface somewhat shiny. Spire ovoid-conical, apex acute (often eroded). Whorls slightly convex, the last slightly flattened above the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Scattered, inconspicuous growth lines. Spiral sculpture: 1 fine subsutural groove, and a low, rather wide, often inconspicuous thread close to the umbilicus, otherwise spiral sculpture virtually absent. Aperture obliquely drop-shaped in outline, acute above, approx. straight or slightly concave on the parietal side, transition from parietal to basal side narrowly rounded, basal side rounded. Peristome rather thick on the parietal side, slightly thickened on the columellar side, basal corner obtusely angular and slightly furrowed oblique to the edge, slightly thickened or not on the basal and palatal side. Umbilicus rimate. Dimensions. Height up to 3.5 mm; width up to 2.6 mm; ratio height/width 1.3–1.4; number of whorls up to 6; height aperture up to 2.0 mm; width aperture up to 1.5 mm.

Distribution in Sabah. Scattered localities in coastal areas and on the islands. Elevation range: 0–100 m. Found in a mangrove swamp. Extralimitally in freshwater and brackish environments, for instance ditches with flowing water, living amphibiously. Distribution elsewhere: Thailand, Indonesia (Sumatra, Java).

Family TRUNCATELLIDAE Gray, 1840

Diagnosis for the Sabah species. Shell dextral, small, elongated conical when juvenile, decollate and approx. cylindrical when adult. Constriction in the last whorl absent. A pore in the inner surface, close to the suture and to the aperture, absent. Color white to pale corneous to red-brown, sometimes banded. Sculpture absent or consisting of radial ribs. Aperture without teeth. Peristome thickened, spreading. Umbilicus covered by the peristome. Operculum corneous, obliquely elliptic or ovate, without a peg on the inside, with few whorls; nucleus strongly excentric.

Note. Juveniles elongated-conical before shedding the top part of the shell.

Genus *Truncatella* Risso, 1826

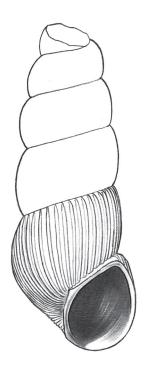
Truncatella guerinii A & J B Villa, 1841

(fig. 77, map 14b)

Villa & Villa 1841: 59; Clench & Turner 1948: 167, 200; Kobelt & Von Möllendorff 1897c: 76; Vermeulen & Whitten 1998: 54; Schilthuizen et al. 2011: 4; Tan et al. 2012: 69; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 65; Foon et al. 2018: 96. – Type from Reunion.

Truncatella marginata Küster 1855: 12; Issel 1874: 452; Tenison Woods 1888: 1077; Godwin-Austen 1889: 354; Kobelt & Von Möllendorff 1897c: 76; Von Martens 1908: 258; Phung et al. 2017: 65. – Type from Malaysia, 'Labuan'.

Description. Shell small, decollated when adult, thick, opaque, almost white to pale corneous to red-brown with or without a pale band below the suture. Surface somewhat shiny. Spire narrowly fusiform with a slightly protruding, rounded apex in juveniles, adults after 1 decollating event subcylindrical, slightly tapering towards the apex, aperture somewhat protruding laterally. Whorls moderately convex, last whorls slightly convex. Sculpture. Protoconch with very fine, densely placed, low, rounded radial riblets. Teleoconch. Radial sculpture: Either with distinct, (rather) densely placed, evenly spaced, rather low and wide ribs with a rounded crest on at least part of the shell, or without ribs, although a crenulation is usually present below the suture. Spiral sculpture absent. Aperture obliquely ovate, narrowly rounded above. Peristome almost white, thickened all around, spreading on the parietal



side. Umbilicus closed; a rounded peripheral ridge often present. Dimensions. Height 6.8–9.2 mm after decollation; width 3.0–3.8 mm (2.2–3.2 mm without the protruding aperture); ratio height/width 2.2–2.5 after decollation; number of whorls 3 3/4–4 1/4 after decollation; height aperture 2.0–2.8 mm; width 1.8–2.3 mm.

Distribution in Sabah. Rather common, localities in W, in coastal areas an on the islands. Elevation: 0 m. Sandy beaches, above the floodmark, among dead leaves and dry vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Coasts of Indian and Pacific Ocean.

Variability. The name Truncatella marginata refers to specimens without radial ribs, or inconspicuous ones. In Sabah material intermediates between ribbed and smooth shells are common, including partially ribbed shells, and shells with the radial ribs reduced to a crenulation below the suture.

Note. The absence of the species on the E coast seems unlikely; we cannot explain why we have no records.

Fig. 77. *Truncatella guerini* A & J B Villa, 1841, frontal view, shell 8.9 mm high.

Family **HELICINIDAE** Férussac, 1822

Diagnosis for the Sabah species. Shell dextral, (very) small, low conical to lenticular. Constriction in the last whorl absent. A pore in the inner surface, close to the suture and to the aperture, absent. Color white to yellow to orange, sometimes with spiral bands. Sculpture (rather) inconspicuous. Aperture without teeth. Peristome thickened and usually spreading (not in *Aphanoconia borneensis*), widely expanded over the parietal side and covering a substantial part of the lower surface of the shell. Umbilicus covered by the peristome. Operculum calcareous, sub-triangular, without a peg on the inside, uncoiled; nucleus strongly excentric.

Notes. 1.The widely expanded and thickened parietal peristome distinguishes helicinid shells from Stylom-matophora with lenticular shells (for instance of the families Ariophantidae, Dyakiidae, Trochomorphidae).

- 2. Next to the various types of spiral sculpture described below, most species locally display a minute, patchy striation approximately perpendicular to the radial sculpture. This is not mentioned in the species descriptions.
 - 3. Corroded shells display a very fine, dense, evenly spaced radial ribbing which is not visible in fresh shells.
- 4. Revised by Wagner (1907–1911). Morphological diagnostic sets for the genera are unclear; therefore, we give diagnostic character cross diagnoses on species level only.

Genus Aphanoconia A J Wagner, 1905

Aphanoconia borneensis (E Von Martens, 1864)

(fig. 78a-c, map 14c)

Wagner 1905: 403; 1909 (1907–1911): 175; Thompson & Dance 1983: 128. – *Helicina borneensis* Von Martens 1864a: 120; Pfeiffer 1865: 238; G B Sowerby II 1866: 286; Von Martens 1867: 171; Issel 1874: 444; Reeve 1873 (1874): Pl. 30, sp. 267; Godwin-Austen 1889: 352. – Type from Indonesia, Kalimantan, 'W Borneo, Singkawang'.

[Not Aphanoconia borneensis auct. Schilthuizen & Vermeulen 2003a: 95; = Sulfurina martensi (Issel)].

Cross diagnosis. Identified among Sabah Helicinidae by the not-spreading palatal and basal peristome. Also, it is generally smaller (shell width 3.8–4.1 mm, versus 4.3–9.5 mm).

Description. Shell very small, rather thin, opaque, uniformly white to (orange-)corneous. Surface (slightly) shiny above. Spire low-conical with slightly convex sides. Whorls: Apical whorls convex, outer whorls almost flat above the periphery, slightly convex below; periphery narrowly rounded. Sculpture. Radial sculpture: Rather distinct, densely placed but unevenly spaced growth lines, locally grading into fine riblets. Spiral sculpture: Sometimes present on parts of the shell, particularly on the first teleoconch whorls and on the lower surface, consisting of unevenly spaced, fine, inconspicuous, densely placed grooves; and up to 4 low, inconspicuous, thin, rounded threads (corresponding with erose crests on the periostracum). Next to this, patches of a very fine granulation (just visible at 40x magnification) may be present. Aperture: Peristome on the palatal and basal side somewhat thickened but not or hardly spreading, double or triple, separated by furrows; basal corner slightly protruding, adjacent parietal callus without a marginal ridge, or with a slight one. Dimensions. Height 2.5–2.7 mm; width 3.8–4.1 mm, ratio height/width 0.64–0.68; diameters of the first three whorls 0.8–1.0 mm, 1.5–1.8 mm, 2.5–3.1 mm respectively; number of whorls 3 5/8–4; height aperture 1.4–1.7 mm; width aperture 1.8–2.0 mm.

Distribution in Sabah. Pulau Mataking only, off Semporna. Elevation range: 0–100 m. In low forest on lime-stone bedrock. Also in Kalimantan. Endemic to Borneo.

Aphanoconia usukanensis (Godwin-Austen, 1889)

(fig. 78d–e, 79a, map 14d)

Thompson & Dance 1983: 128; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 66; Foon et al. 2018: 96. – *Helicina usukanensis* Godwin-Austen 1889: 352; Smith 1895: 100, 125; Von Martens 1908: 259. – Type from Malaysia, Sabah, West Coast Prov., Usukan island (off Kota Belud).

Aphanoconia trichroa Wagner 1905: 400; 1909 (1907–1911): 173; Thompson & Dance 1983: 129; Schilthuizen et al. 2011: 4. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

Helicina contermina auct. Smith 1894c: 59.

Helicina (Pleuropoma) sp. Von Möllendorff 1894: 214. [Not *Helicina contermina* Kobelt].

Cross diagnosis. Shares the presence of a peripheral keel with *Geophorus agglutinans*, differs by the more obtuse keel and by the shinier upper surface of the shell, without granulose sculpture. Also, it is generally smaller than *Geophorus agglutinans* (shell width 5.0–7.2 mm, versus 7.1–9.5 mm).

Description. Shell small, rather thin, opaque, white, yellow or orange-brown, usually with a white periphery and a thin, brownish spiral band immediately below, sometimes with a vaguely outlined, paler spiral band below the suture. Surface shiny. Spire low-conical with slightly convex sides. Whorls: Apical whorls slightly convex, outer whorls (nearly) flat above the periphery, slightly convex below; periphery somewhat obtusely to somewhat truncately keeled, keel sometimes slightly protruding. Sculpture. Radial sculpture: Inconspicuous growth lines, grading into a very fine, inconspicuous striation, locally into fine and densely placed ribs. Spiral sculpture: Usually present, at least locally, on the first teleoconch whorls, often continuing on the outer whorls, consisting of 2–4 low, inconspicuous, rounded threads (corresponding with erose crests on the periostracum), on the last whorl as threads, rows of slight swellings or as shallow grooves. Granulation absent. Aperture: Peristome on the palatal and basal side somewhat thickened and distinctly spreading, single; basal corner slightly protruding, adjacent parietal callus without a marginal ridge, or with a slight one. Dimensions. Height 3.2–4.7 mm; width 5.0–7.2 mm, ratio height/ width 0.59–0.67; diameters of the first three whorls 0.8–1.2 mm, 1.8–2.2 mm, 3.0–3.9 mm respectively; number of whorls 3 3/4–4 1/8; height aperture 2.0–2.7 mm; width aperture 2.6–3.6 mm.

Distribution in Sabah. Rather common in coastal areas and on the islands; inland in lower Kinabatangan only. Elevation range: 0–400 m. Primary and secondary forest, coastal shrubland on limestone and volcanic bedrock. Also in Kalimantan. Distribution elsewhere: Philippines (Palawan and Sulu archipelago).

Genus Geophorus Fischer, 1885

Note. Geophorus oxytropis (Gray, 1839) occurs in E Kalimantan and may be found in Sabah. It differs from *G. agglutinans* by its conical spire, with straight sides, and by a more distinctly pinched peripheral keel.

Geophorus agglutinans (G B Sowerby II, 1842)

(fig. 78f, map 14e)

Geophorus agglutinans agglutinans (G B Sowerby II) Wagner 1908 (1907–1911): 140; Zilch 1979 (1978): 379; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data. – *Helicina agglutinans* G B Sowerby II 1842a: 7; 1842b: 11; Pfeiffer 1852b: 394; 1858: 217; Reeve 1873 (1874): Pl. 25, sp. 220; Pfeiffer 1876: 282. – Type from Philippines.

Geophorus agglutinans eos Wagner 1908 (1907–1911): 143; Thompson & Dance 1983: 128. – Type from Indonesia, Kalimantan, 'gunung Sekarat'.

Helicina (Geophorus) lazarus auct. Von Möllendorff 1894: 214.

[Not Helicina lazarus G B Sowerby II].

Cross diagnosis. Identified among Sabah Helicinidae by the acute peripheral keel, in combination with the dull, 'sanded' upper surface of the shell.

Description. Shell small, rather thin, opaque, white, lemon yellow to red-brown, sometimes with a slightly darker apex, sometimes with a paler periphery. Surface dull above, shiny below. Spire low-conical with slightly convex sides and slightly protruding apex. Whorls: Apical whorls convex, outer whorls slightly convex above and below the periphery. Periphery acutely angular, often slightly pinched in the outer whorls. Sculpture. Radial sculpture: Fine and unevenly spaced growth lines, often grading into slightly raised riblets, or on the upper surface often appearing as pale lines. Spiral sculpture absent. Upper surface with a fine (visible at 40x magnification) granular sculpture giving the shell surface a 'sanded' appearance. Aperture: Peristome on the palatal and basal side somewhat thickened and distinctly spreading, single; basal corner protruding, adjacent parietal callus with a marginal ridge. Dimensions. Height 4.4–5.8 mm; width 7.1–9.5 mm, ratio height/width 0.58–0.63; diameters of the first three whorls 1.2–1.3 mm, 2.2–2.4 mm, 3.9–4.5 mm respectively; number of whorls 4 1/4–4 3/4; height aperture 2.1–3.0 mm; width aperture 3.5–5.0 mm.

Distribution in Sabah. Scattered localities in E. Elevation range: 0–400 m. Primary and secondary forest on limestone bedrock. Also in Kalimantan. Distribution elsewhere: Philippines, Indonesia (Sumba, Timor).

Variability. The Borneo material is smaller than the type subspecies. Sabah material is intermediate between subsp. *eos* Wagner, and subsp. *cyrtopoma* (Von Möllendorff, 1887), from the Philippines, see Wagner (1907–1911: 140).

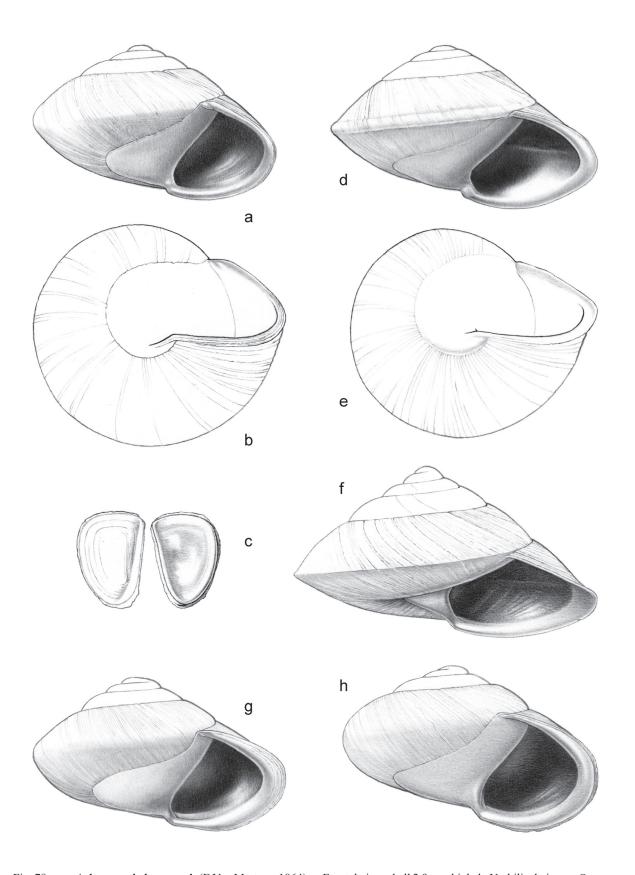


Fig. 78, a–c. *Aphanoconia borneensis* (E Von Martens, 1864), a. Frontal view, shell 2.9 mm high, b. Umbilical view, c. Operculum, left: Inside, right: Outside; d–e. *Aphanoconia usukanensis* (Godwin-Austen, 1889), d. Frontal view, shell 4.7 mm high, e. Umbilical view; f. *Geophorus agglutinans* (G B Sowerby II, 1842), frontal view, shell 5.5 mm high; g–h. *Sulfurina martensi* (Issel, 1874), frontal view, g. Shell 3.0 mm high, h. Shell 3.2 mm high.

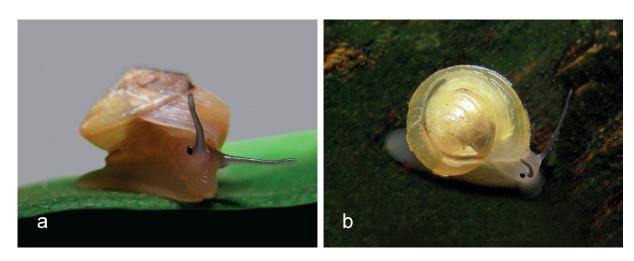


Fig. 79, a. Aphanoconia usukanensis (Godwin-Austen, 1889); b. Sulfurina martensi (Issel, 1874).

Genus Sulfurina Von Möllendorff, 1893

Sulfurina martensi (Issel, 1874)

(fig. 78g–h, 79b, map 14f)

Wagner 1905: 374; 1907 (1907–1911): 24; Solem 1964: 9; Saul 1967: 110; Thompson & Dance 1983: 128; Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53. – *Helicina martensi* Issel 1874: 444; Dohrn 1889: 57; Godwin-Austen 1889: 353; Smith 1894b: 464; 1894c: 59; Von Martens 1908: 259; Saul 1967: 109. – *Helicina (Sulfurina) martensi* (Issel) Von Möllendorff 1894: 214. – Type from Malaysia, Labuan.

Aphanoconia borneensis auct. Schilthuizen & Vermeulen 2003a: 95.

Sulfurina euchromia auct. Clements et al. 2008: 2762.

Sulfurina sp. Schilthuizen & Rutjes 2001: 420.

[Not Aphanoconia borneensis (E Von Martens)].

[Not Sulfurina euchromia Wagner].

Cross diagnosis. Shares the narrowly rounded periphery with *Aphanoconia borneensis*, differs by the distinctly spreading palatal and basal peristome. Also, it is generally larger, with more rapidly expanding whorls (diameter third whorl 3.4–4.3 mm, versus 2.5–3.1mm).

Description. Shell small, rather thin, opaque, uniformly white to lemon yellow, or orange-brown with a slightly paler periphery. Surface shiny. Spire approx. conical with straight or slightly convex sides. Whorls: Apical whorls convex, outer whorls slightly convex with slightly impressed sutures above the periphery, slightly convex below. Periphery (narrowly) rounded. Sculpture. Radial sculpture: Fine, inconspicuous growth lines, grading into fine striation, or locally into fine, densely placed riblets. Spiral sculpture absent, or up to 3 inconspicuous lines of slightly rougher sculpture above the periphery, and up to 4 shallow grooves or rows of shallow depressions below. Granulation absent. Aperture: Peristome on the palatal and basal side somewhat thickened and distinctly spreading, often inconspicuously double, separated by a slight furrow close to the edge; basal corner slightly protruding, adjacent parietal callus without a marginal ridge, or with a slight one. Dimensions. Height 3.0–4.9 mm; width 4.3–7.8 mm, ratio height/width 0.59–0.77; diameters of the first three whorls 0.9–1.2 mm, 1.9–2.2 mm, 3.4–4.3 mm respectively; number of whorls 3 1/2–4 1/8; height aperture 2.0–3.1 mm; width aperture 2.2–3.6 mm.

Distribution in Sabah. Widespread, common, particularly in E. Elevation range: 0–1100 m. In (disturbed) primary forest, secondary woodland, degraded shrubland; on limestone bedrock, sometimes on sandstone/shale bedrock. Also in Kalimantan. Distribution elsewhere: Philippines (see note), Indonesia (Sumatra).

Note. Sulfurina citrina (Grateloup, 1840), S. citrinella (Von Möllendorff, 1893) and S. euchromia Wagner, 1905, see Wagner (1907–1911: 19–23), from Philippines (including the Tawi-Tawi group of the Sulu archipelago) and Indonesia (Sulawesi), are possibly identical with S. martensi. This would extend the range of the species to the east.

Family HYDROCENIDAE Troschel, 1857

(By M Z Khalik & J J Vermeulen)

Diagnosis for the Sabah species. Shell dextral, minute or very small, ovoid to conical with rounded apex. Constriction in the last whorl absent. A pore in the inner surface, close to the suture and to the aperture, absent. Color white or yellow to orange-red. Radial and/or spiral sculpture usually conspicuous, sculpture sometimes inconspicuous or almost absent (Georissa filiasaulae, G. bangueyensis). Peristome thickened, not spreading, wide and conspicuous on the parietal side, but not much spreading over the lower surface of the shell. Umbilicus usually closed. Operculum calcareous, with few whorls, with a peg on the inside along the parietal edge which protrudes beyond the margin, obliquely elliptic or ovate; nucleus strongly excentric, growth lines concentric.

Note. The wide, conspicuous, sometimes thickened, sometimes impressed parietal peristome, covering the umbilical area, distinguishes Hydrocenidae from *Acmella* and *Anaglyphula* (Assimineidae), and from *Pupisoma* and *Ptychopatula* (Vertiginidae).

Genus Georissa W T Blanford, 1864

Notes. 1. Individuals with a relatively weak sculpture occur in most species. These may be difficult to identify, particularly if they are not found together with sculptured specimens of the same species.

- 2. Juveniles may develop a thickened peristome and look deceptively like adult shells.
- 3. The Borneo species are revised in Khalik et al. (2018, 2019).

KEY TO THE GROUPS

- 1 Radial ribs with upright, scale-like projections arranged in one or more spiral rows
 - 2 Upper spiral row of scales situated just below the suture

Group 1

2 – Upper spiral row of scales situated near the periphery

Group 2

- 1 Radial ribs without projections (a subsutural thread with fine scales may be present), or radial ribs absent
 - 3 Radial sculpture predominant, (rather) distinct

Group 3

- 3 Either spiral sculpture predominant (spiral threads coarse to very fine, but more distinct than the radial sculpture which consists at most of locally raised growth lines); or all sculpture very inconspicuous
 - 4 Spiral sculpture at the end of the penultimate whorl consisting of 5–7 thick spiral threads (sometimes with a few more much finer threads in between). Shell height 1.40–1.89 mm; width 1.12–1.37 mm

Group 4

- 4 Spiral sculpture at the end of the penultimate whorl consisting of 8–25 thin spiral threads, if spiral sculpture at the end of the penultimate whorl consisting of 8–11 spiral threads then shell height 1.00–1.33 mm and width 0.77–0.96 mm
 - 5 Shell height 1.4 mm or less

Group 5

5 – Shell height more than 1.4 mm

Group 6

Group 1

Georissa filiasaulae Haase & Schilthuizen 2007

(fig. 80a–d, map 15a)

Haase & Schilthuizen. 2007: 2016; Clements et al. 2008: 2762; Schilthuizen et al. 2012: 727; Khalik et al. 2019:

66. – Type from Malaysia, Sabah, Sapulut valley, Gua Sanaron.

Georissa filiasaulae, unavailable name, Clements et al. 2006: 736.

Georissa n.sp. Schilthuizen et al. 2005: 133.

Cross diagnosis. Resembles *Georissa saulae* in general shell shape, including the whorl profile and the position of the (uppermost) spiral row of scales, but differs by the white, somewhat translucent shell with inconspicuous sculpture only.

Description. Shell minute, solid, translucent, white. Surface slightly shiny. Spire conical with rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, narrowly but distinctly shouldered just below the suture. Sculpture. Protoconch densely rugulose with partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Unevenly spaced growth lines, locally somewhat raised or developed into low, narrow riblets, growth lines at small intervals with a small, scale-like projection on the shoulder, close to the suture, on the last half-whorl often with a second small scale-like projection lower down, above the periphery. Spiral sculpture: Fine, inconspicuous, moderately and unevenly spaced, thin, low threads, which run approx. parallel to the suture just below the suture and below the periphery, but elsewhere slightly

obliquely downwards (in the direction of the aperture). Aperture approx. semi-elliptic, parietal side slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.21–1.54 mm; width 1.17–1.38 mm; ratio height/width 1.08–1.27; number of whorls 2 1/2–3; height aperture 0.67–0.79 mm; width aperture 0.69–0.83 mm; ratio height/width aperture 0.93–0.97.

Distribution in Sabah. Sapulut only. Elevation range: 300-400 m. In caves. Endemic to Sabah.

Variability. Known from two localities. At Gua Sanaron, narrow zones with shells of intermediate morphology occur where the cave-dwelling *Georissa filiasaulae* meets outside-living *G. saulae*; see Schilthuizen et al. (2005: 134, fig. 1). In the Tinahas population morphological intermediates commonly occur, see Schilthuizen et al. (2012).

Georissa saulae (Van Benthem Jutting, 1966)

(fig. 80e-h, map 15b)

Thompson & Dance 1983: 118; Schilthuizen 2004: 94; Schilthuizen et al. 2005: 133; Haase & Schilthuizen 2007: 217; Clements 2008: 2762; Schilthuizen et al. 2012: 727; Phung et al. 2017: 68. – *Hydrocena saulae* Van Benthem Jutting 1966: 40; Saul 1967: 109. – Type from Malaysia, Sabah, Lian Cave in Crocker range. *Georissa* sp. Liew et al. 2010: Online Supporting Information, Appendix S1.

Description. Shell minute, solid, slightly translucent to opaque, red to brown. Surface dull. Spire conical with rounded apex, last whorl slightly turned inwards or not. Whorls convex, evenly rounded, narrowly shouldered just below the suture. Sculpture. Protoconch densely rugulose with partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture predominant: Distinct, rather widely and slightly unevenly spaced, narrow ribs, on the last whorl each rib with 4–5 scale-like projections, the lower-most lowest and widest, the uppermost on the shoulder, close to the suture, the one below this highest and most prominent. Spiral sculpture: Fine, widely and unevenly spaced, thin, low threads, which run slightly obliquely downwards (in the direction of the aperture) around the periphery and above but run parallel to the suture below the periphery. Aperture approx. semi-elliptic, parietal side slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.32–1.86 mm; width 1.14–1.48 mm; ratio height/width 1.12–1.26; number of whorls 2 1/2–3 1/4; height aperture 0.58–0.77 mm; width aperture 0.70–0.90 mm; ratio height/width aperture 0.76–0.92.

Distribution in Sabah. Rare in W: Crocker range, Pun Batu, Sapulut. Elevation range: 300–700 m. Primary forest, (degraded) secondary forest, coastal woodland. Endemic to Sabah.

Variability. See note under Georissa filiasaulae.

Group 2

Georissa kinabatanganensis Khalik, Hendriks, Vermeulen & Schilthuizen, 2018 (fig. 80i–l, map 15a) Khalik et al. 2018: 47. – Type from Malaysia, Sabah, Kinabatangan river valley, Batu Keruak.

Cross diagnosis. Differs from *Georissa scalinella* and *G. sepulutensis* by the presence of two spiral rows (versus one row) of scales on the first half of the last whorl. Also, it is relatively wide: ratio height/width 0.85–0.99, versus ratio height/width 0.94–1.15.

Description. Shell minute, solid, approx. opaque, orange. Surface dull or slightly shiny. Spire depressed-conical with rounded apex, last whorl hardly turned inwards. Whorls prominently convex, evenly rounded or slightly and obtusely angular above the periphery. Sculpture. Protoconch densely rugulose with densely placed, partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Densely placed and unevenly spaced, raised growth lines, at uneven intervals developing in narrow, low riblets, the riblets on the last whorl each with 2 scale-like, rounded projections, one below the periphery, and one, the most prominent, above the periphery. Spiral sculpture: Rather distinct, somewhat wavy, widely and somewhat unevenly spaced, rather thin and low threads which run parallel to the suture: On the last whorl 5–9 above the upper row of scales on the radial sculpture, 3–4 in between the two rows, 7–9 below the lower row. Aperture obovate with the basal corner obtusely angular, parietal side approx. straight. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.00–1.32 mm; width 1.13–1.37 mm; ratio height/width 0.85–0.99; number of whorls 2–2 1/4; height aperture 0.54–0.66 mm; width aperture 0.75–0.86 mm; ratio height/width aperture 0.65–0.80.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In primary and secondary forest on limestone bedrock. Endemic to Sabah.

Georissa scalinella (Van Benthem Jutting, 1966)

(fig. 81a–d, map 15a)

Thompson & Dance 1983: 119; Clements et al. 2008: 2762; Phung et al. 2017: 68; Khalik et al. 2018: 26. – Hy-

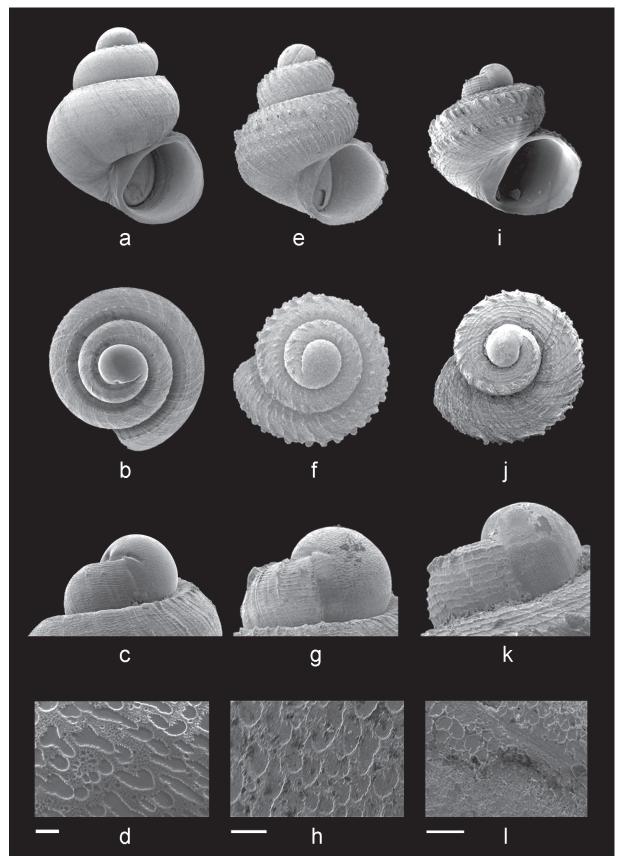


Fig. 80, a–d. *Georissa filiasaulae* Haase & Schilthuizen, 2007, a. frontal view, shell 1.6 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa saulae* (Van Benthem Jutting, 1966), e. frontal view, shell 1.2 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa kinabatanganensis* Khalik et al., 2018, i. frontal view, shell 0.9 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: $10 \ \mu m$.

drocena scalinella Van Benthem Jutting 1966: 39; Saul 1967: 109. – Type from Malaysia, Sabah, Kirk's cave near Lahad Datu.

[Not Georissa scalinella auct. Schilthuizen et al. 2005: 134–135; = Georissa sepulutensis Khalik et al.].

Cross diagnosis. Differs from *Georissa sepulutensis* by the last whorl, which is obtusely angular at the periphery, almost flat above, and slightly convex below. It is also larger: Shell height 1.56–1.88 mm, versus 1.11–1.52 mm.

Description. Shell minute, solid, approx. opaque, orange. Surface dull or slightly shiny. Spire conical with narrowly rounded apex, last whorl hardly turned inwards. Whorls prominently convex, slightly and obtusely angular at periphery, almost flat above, widely rounded below. Sculpture. Protoconch densely rugulose with densely placed, partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Densely placed and unevenly spaced, raised growth lines, at uneven intervals developing in narrow, low riblets, the riblets on the last whorl each with 1 scale-like, rounded projection on the periphery. Spiral sculpture: Rather distinct, wavy, widely and somewhat unevenly spaced, rather thin and low threads which run parallel to the suture: On the last whorl 10–14 above the row of scales on the radial sculpture, 18–21 below. Aperture obovate with the basal corner obtusely angular, parietal side approx. straight. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.56–1.88 mm; width 1.46–1.72 mm; ratio height/width 1.03–1.15; number of whorls 2–2 1/4; height aperture 0.78–0.94 mm; width aperture 0.97–1.18 mm; ratio height/width aperture 0.71–0.89.

Distribution in Sabah. Rare in S and E: Sapulut, Baturong-Madai, Lahad Datu. Elevation range: 100–600 m. Primary forest, coastal woodland. Endemic to Sabah.

Georissa sepulutensis Khalik, Hendriks, Vermeulen & Schilthuizen, 2018 (fig. 81e–h, map 15c)

Khalik et al. 2018: 49. – Type from Malaysia, Sabah, Sapulut valley, Gua Pungiton. *Georissa scalinella* auct. Schilthuizen et al. 2005: 134–135. [Not *Georissa scalinella* Van Benthem Jutting].

Description. Shell minute, solid, slightly translucent to approx. opaque, red. Surface dull or slightly shiny. Spire conical with narrowly rounded apex, last whorl slightly turned inwards. Whorls prominently convex, approx. evenly rounded. Sculpture. Protoconch densely rugulose with densely placed, partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Densely placed and unevenly spaced, raised growth lines, at uneven intervals developing in narrow, low riblets, the riblets on the last whorl each with 1 small, scale-like, rounded projection on the periphery. Spiral sculpture: Rather distinct, wavy, widely and unevenly spaced, rather thin and low threads which run parallel to the suture: On the last whorl c. 7 above the row of scales on the radial ribs, 18–21 below. Aperture obovate with the basal corner obtusely angular, parietal side approx. straight. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.11–1.52 mm; width 1.11–1.37 mm; ratio height/width 0.94–1.11; number of whorls 2–2 3/4; height aperture 0.62–0.81 mm; width aperture 0.76–0.96 mm; ratio height/width aperture 0.72–0.87.

Distribution in Sabah. Sapulut only. Elevation range: 300–500 m. Primary and secondary forest. On limestone bedrock. Endemic to Sabah.

Group 3

Georissa borneensis E A Smith, 1895

(fig. 81i–l, map 15c)

Smith 1895: 126; Von Martens 1908: 259; Thompson & Dance 1983: 122; Clements et al. 2008: 2762; Khalik et al. 2019: 50. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Uniquely identified within Group 3 by its whorl profile: Narrowly rounded at the periphery, and slightly flattened above and below. The other species have evenly rounded whorls.

Description. Shell minute to very small, solid, opaque, white to pale orange. Surface dull. Spire conical with narrowly rounded apex, last whorl slightly turned inwards. Whorls convex, first whorl evenly rounded, last whorl narrowly rounded at periphery, slightly flattened above and shouldered just below the suture, slightly flattened below. Sculpture. Protoconch with elongated, partly concatenated, shallow depressions arranged in rows (at 100x magnification). Teleoconch. Radial sculpture: Moderately spaced to densely placed, unevenly spaced, distinct, depressed (on the last whorl) radial ribs with somewhat erose edges. Spiral sculpture subordinate to the radial sculpture, widely and somewhat unevenly spaced, very thin, wavy threads, interrupted by the radial ribs and only locally present or absent on the last whorl; spiral sculpture parallel to the suture. Aperture approx. semi-elliptic

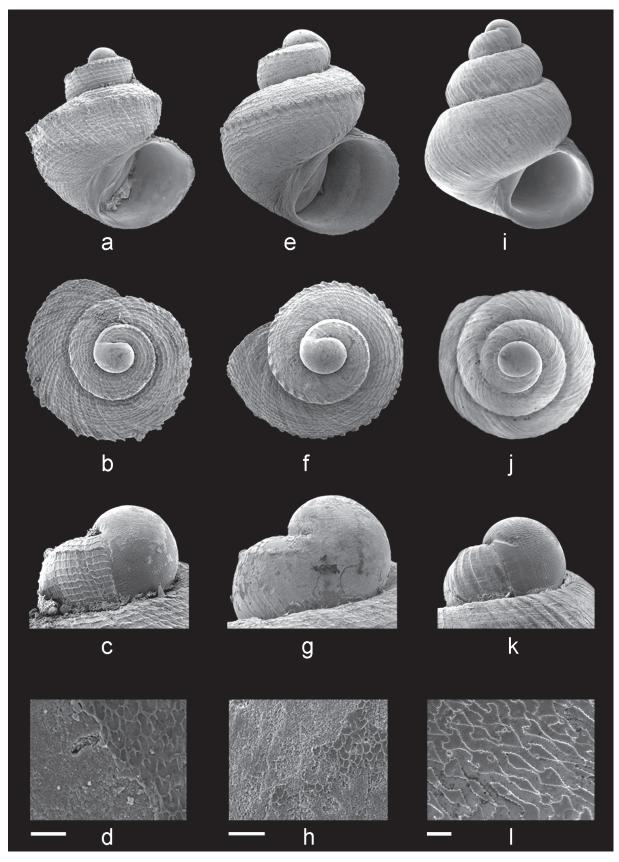


Fig. 81, a–d. *Georissa scalinella* (Van Benthem Jutting, 1966), a. frontal view, shell 1.6 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa sepulutensis* Khalik et al., 2018, e. frontal view, shell 1.3 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa borneensis* E A Smith, 1895, i. frontal view, shell 2.0 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: 10 µm.

with the basal corner somewhat angular, parietal side approx. straight. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.91–2.23 mm; width 1.65–1.82 mm; ratio height/width 1.12–1.28; number of whorls 2 3/4–3 1/2; height aperture 0.82–1.07 mm; width aperture 1.00–1.09 mm; ratio height/width aperture 0.75–1.02.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Georissa corrugata Khalik, Hendriks, Vermeulen & Schilthuizen, 2019 (fig. 82a–d, map 15d) Khalik et al. 2019: 52. – Type from Malaysia, Sabah, Kinabatangan river valley, Batu Tomanggong.

Cross diagnosis. Differs primarily from *Georissa similis* by the protoconch sculpture which consists of shallow grooves (just visible at 50x magnification, but better at 100x). It also differs by the more widely spaced radial ribs.

Description. Shell minute, solid, approx. opaque or slightly translucent, white. Surface dull or slightly shiny. Spire conical with rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, narrowly shouldered just below the suture. Sculpture. Protoconch with almost uninterrupted, sometimes branching, shallow, linear depressions (at 100x magnification). Teleoconch. Radial sculpture: Rather widely to moderately spaced, unevenly distributed, distinct, rather low and wide radial ribs, on the last whorl locally fused to more prominent ridges with uneven crests, some of which are depressed. Spiral sculpture subordinate to the radial sculpture, widely and somewhat unevenly spaced, thin, wavy threads, interrupted by the radial sculpture on the last whorl, only partially so on the penultimate whorl; spiral sculpture parallel to the suture. Aperture approx. semi-elliptic with the basal corner somewhat angular, parietal side approx. straight or slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.00–1.43 mm; width 0.88–1.20 mm; ratio height/width 1.10–1.29; number of whorls 2 1/4–3; height aperture 0.47–0.63 mm; width aperture 0.52–0.73 mm; ratio height/ width aperture 0.85–0.98.

Distribution in Sabah. Scattered localities in E: Lower Kinabatangan, Tabin, Baturong-Madai; elsewhere in Sapulut only. Elevation range: 0–500 m. Primary and secondary forest on limestone bedrock. Always in low numbers. Endemic to Sabah.

Georissa everetti E A Smith, 1895

(fig. 82e-h, map 15c)

Smith 1895: 125; Thompson & Dance 1983: 120; Khalik et al. 2019: 54; Marzuki et al. 2021: 42. – Type from Malaysia, Sarawak 'Rumbang'.

Cross diagnosis. Consistently larger than *Georissa corrugata* and *G. similis*: Shell height 1.82–2.23 mm, width 1.52–1.75 mm; versus shell height 1.00–1.43 mm, width 0.88–1.20 mm.

Description. Shell very small, solid, approx. opaque, orange to red. Surface dull. Spire conical with narrowly rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, narrowly shouldered just below the suture. Sculpture. Protoconch with shallow, circular to elliptic depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Rather widely and unevenly spaced, rather distinct but low and narrow radial ribs which often develop into a small knob or crest over the shoulder, with less prominent, thinner riblets in between. Spiral sculpture slightly subordinate, widely and somewhat unevenly spaced, thin, wavy threads, which form a small knot where they cross the more prominent radial ribs; the spiral sculpture runs slightly obliquely downwards (in the direction of the aperture) around the periphery and above, but below the periphery it runs parallel to the suture. Aperture approx. semi-elliptic, basal corner somewhat angular, parietal side approx. straight or slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.82–2.23 mm; width 1.52–1.75 mm; ratio height/width 1.16–1.30; number of whorls 2 3/4–3 1/4; height aperture 0.92–1.05 mm; width aperture 0.96–1.09 mm; ratio height/width aperture 0.89–0.99.

Distribution in Sabah. Sapulut only. Elevation range: 400–500 m. Primary and secondary forest on limestone bedrock. Always in low numbers of individuals. Also in Sarawak. Endemic to Borneo.

Georissa similis E A Smith, 1893

(fig. 82i–l, map 15b)

Smith 1893b: 351; Von Martens 1908: 259; Thompson & Dance 1983: 126; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Khalik et al. 2019: 72. – Type from Malaysia, Sabah, 'Gomanton Hill'.

Hydrocena gomantongensis auct. Solem 1964: 8.

Georissa sp. '3' Clements et al. 2008: 2762.

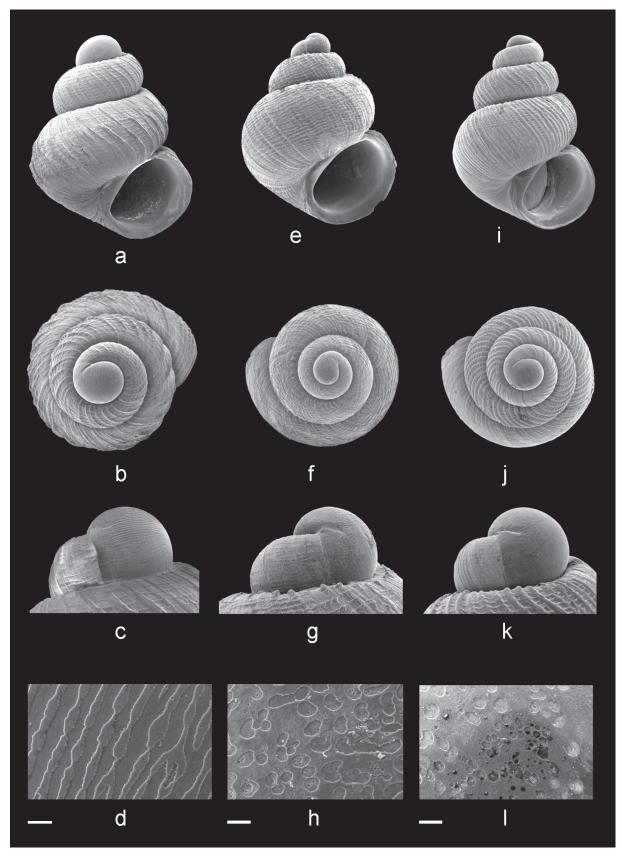


Fig. 82, a–d. *Georissa corrugata* Khalik et al., 2019, a. frontal view, shell 1.4 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa everetti* E. A. Smith, 1895, e. frontal view, shell 2.0 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa similis* E A Smith, 1893, i. frontal view, shell 1.4 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: $10~\mu$ m.

Georissa sp. 'bo-03' Schilthuizen & Vermeulen 2003a: 95. Georissa sp. 'V 1829' Schilthuizen et al. 2013: Online supplementary data. [Not Georissa gomantongensis (E A Smith)].

Description. Shell minute, solid, approx. opaque, red. Surface dull or slightly shiny. Spire conical with rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, narrowly shouldered just below the suture. Sculpture. Protoconch with locally clustered, shallow, circular to elliptic depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture: Moderately spaced but on the last whorl rather densely placed, locally rather evenly distributed but elsewhere clustered, rather distinct, low and rather wide radial ribs. Spiral sculpture subordinate to the radial sculpture but not inconspicuous, moderately and somewhat unevenly spaced, rather thin, slightly wavy threads, which are interrupted where they cross the radial ribs; spiral sculpture parallel to the suture. Aperture approx. semi-elliptic, parietal side approx. straight to slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 0.96–1.44 mm; width 0.85–1.06 mm; ratio height/width 1.13–1.36; number of whorls 2 1/2–3 1/4; height aperture 0.49–0.64 mm; width aperture 0.50–0.67 mm; ratio height/width aperture 0.85–0.98.

Distribution in Sabah. Rather common in E. Elevation range: 0–300 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Group 4

Georissa trusmadi Khalik, Hendriks, Vermeulen & Schilthuizen, 2019 (fig. 83a–d, map 15b) Khalik et al. 2019: 58. – Type from Malaysia, Sabah, mount Trus Madi, Loloposon Cave.

Description. Shell minute, solid, approx. opaque, orange. Surface dull. Spire somewhat elevated-conical with rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, slightly and narrowly shouldered just below the suture. Sculpture. Protoconch with shallow depressions of uneven shape, size and orientation (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: Approx. 11–14 rather thin spiral threads at the start of the teleoconch, of which 5–7 (counted at the end of the penultimate whorl) develop into thick, high and wide spiral cords with a rounded, unevenly tubercular crest; the other, rather thin threads occur scattered in between; basal area with more threads, decreasing in thickness towards the umbilicus. Aperture approx. semi-elliptic, parietal side approx. straight to slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.40–1.89 mm; width 1.12–1.37 mm; ratio height/width 1.22–1.38; number of whorls 2 3/4–3 1/2; height aperture 0.59–0.72 mm; width aperture 0.66–0.79 mm; ratio height/width aperture 0.85–0.91.

Distribution in Sabah. Highlands: Mount Trus Madi only. Elevation range: 1000–1100 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Group 5

Check also:

Georissa filiasaulae (Group 1). Relatively smooth shells may key out here but differ by the presence of a shoulder, just below the suture, with minute knobs or scales.

Georissa bangueyensis E A Smith, 1895

(fig. 83e–h, map 15e)

Smith 1895: 100, 125; Thompson & Dance 1983: 126; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96; Khalik et al. 2019: 78. – Type from Malaysia, Sabah, Banggi island.

[Not *Georissa bangueyensis* auct. Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; = *Georissa xesta* F G Thompson & Dance].

Description. Shell minute, solid, approx. opaque, red. Surface dull or slightly shiny. Spire somewhat elevated-conical with rounded apex, last whorl slightly turned inwards or not. Whorls convex, evenly rounded, not shouldered below the suture. Sculpture. Protoconch shallowly and often inconspicuously rugulose (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 8–12 moderately and rather evenly spaced, straight, low, rather thin spiral threads on the first teleoconch whorl; at the end of the penultimate whorl the threads are still present, often more prominent above the periphery, but on the last half-whorl most or all have faded; basal area with traces of fine threads near the parietal peristome only. Aperture approx. semi-elliptic, parietal side approx. straight to slightly

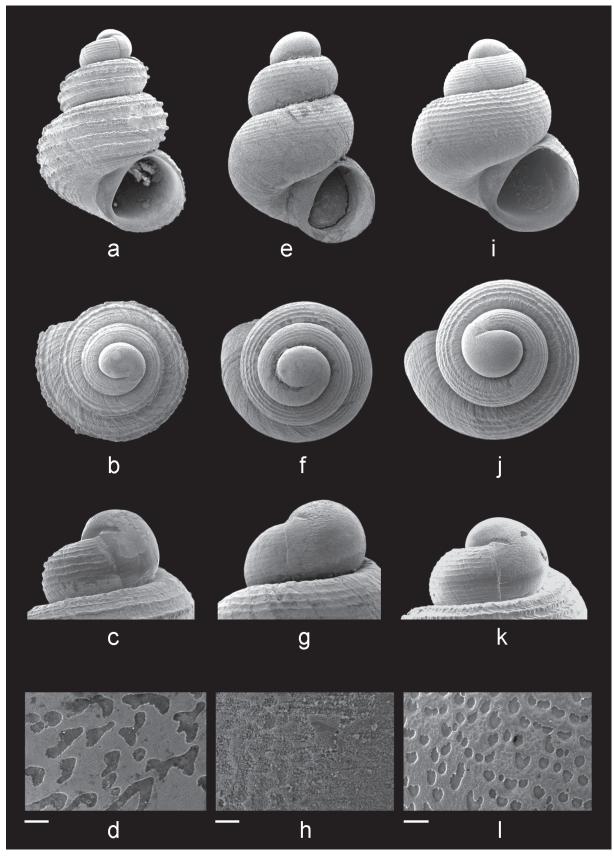


Fig. 83, a–d. *Georissa trusmadi* Khalik et al., 2019, a. frontal view, shell 1.7 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa bangueyensis* E A Smith, 1895, e. frontal view, shell 1.3 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa flavescens* E A Smith, 1895, i. frontal view, shell 0.9 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: $10~\mu m$.

concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.00–1.33 mm; width 0.77–0.96 mm; ratio height/width 1.22–1.42; number of whorls 2 3/4–3; height aperture 0.40–0.53 mm; width aperture 0.45–0.60 mm; ratio height/width aperture 0.81–1.00.

Distribution in Sabah. Scattered localities in N and E: Balambangan and Banggi islands, lower Kinabatangan (common), Ulu Segama. Elevation range: 0–200 m. Primary forest, secondary forest and coastal vegetation on limestone bedrock. Endemic to Sabah.

Georissa flavescens E A Smith, 1895

(fig. 83i–l, map 15f)

Smith 1895: 126; Von Martens 1908: 259; Khalik et al. 2019: 81. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Cross diagnosis. Differs from *Georissa bangueyensis* and *G. xesta* by the finely wavy spiral threads (a character it shares with *G. nephrostoma*). It differs also by its generally wider shell: ratio height/width 1.15–1.26; versus 1.22–1.45.

Description. Shell minute, solid, slightly translucent, orange. Surface slightly shiny. Spire conical with rounded apex, last whorl slightly turned inwards or not. Whorls convex, evenly rounded, slightly shouldered immediately below the suture. Sculpture. Protoconch with shallow depressions of uneven shape and size, some approx. aligned (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 12–16 moderately and rather evenly spaced, distinctly but finely wavy, low, rather narrow spiral threads on the first teleoconch whorl; at the start of the last whorl the threads are still present, widened and somewhat flattened, with neighboring threads wavy in opposite direction below the periphery and therefore meeting at intervals, causing a sculpture of aligned depressions; on the last half-whorl more threads meet while somewhat fading at the same time; basal area with traces of fine threads fading towards the aperture. Aperture semi-elliptic, parietal side approx. straight to slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 0.87–1.20 mm; width 0.73–0.95 mm; ratio height/width 1.15–1.26; number of whorls 2 1/2–2 3/4; height aperture 0.43–0.55 mm; width aperture 0.47–0.58 mm; ratio height/width aperture 0.82–0.95.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. Primary and secondary forest. Endemic to Sabah.

Georissa leucococca Vermeulen, Liew & Schilthuizen, 2015

(fig. 84a–d, map 15f)

Vermeulen et al. 2015: 33; Marzuki & Foon 2016: 317; Khalik et al. 2019: 59; Marzuki et al. 2021: 44. – Type from Malaysia, Sabah, Interior Prov., Gua Pungiton.

Cross diagnosis. Uniquely identified among Sabah *Georissa* by its small size (shell height 0.62–0.72 mm, versus shell height 0.87 mm or more), in combination with the white color of the shell. It differs from juveniles of other *Georissa* by its impressed umbilical region.

Description. Shell minute, solid, slightly translucent, white. Surface slightly shiny. Spire somewhat depressed-conical, almost ovoid, with broadly rounded apex, last whorl not or hardly turned inwards. Whorls convex, evenly rounded, or slightly more narrowly rounded around the periphery than elsewhere, not or hardly shouldered below the suture. Sculpture. Protoconch with densely placed, shallow, unevenly polygonal depressions (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 11–15 moderately and evenly spaced, slightly wavy, low, thin spiral threads on the first teleoconch whorl, leaving a narrow zone above the suture without spiral sculpture; at the end of the penultimate whorl the threads are still present, with those below the suture most prominent, but on the last half-whorl they gradually disappear; basal area without spiral sculpture. Aperture approx. semi-elliptic, parietal side approx. straight to slightly concave. Umbilicus open, with a narrow space underneath the columellar peristome, or closed, umbilical region somewhat impressed, in juveniles more distinctly impressed. Dimensions. Height 0.62–0.72 mm; width 0.60–0.70 mm; ratio height/width 0.97–1.06; number of whorls 2 1/4–3; height aperture 0.31–0.37 mm; width aperture 0.33–0.38 mm; ratio height/width aperture 0.87–0.97.

Distribution in Sabah. Rare in S and E: Sapulut, Baturong-Madai. Elevation range: 100–500 m. Primary and secondary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Georissa nephrostoma Vermeulen, Liew & Schilthuizen, 2015

(fig. 84e–h, map 16a)

Vermeulen et al. 2015: 34; Khalik et al. 2019: 76. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatagan river valley, Batu Keruak 2 near Sukau.

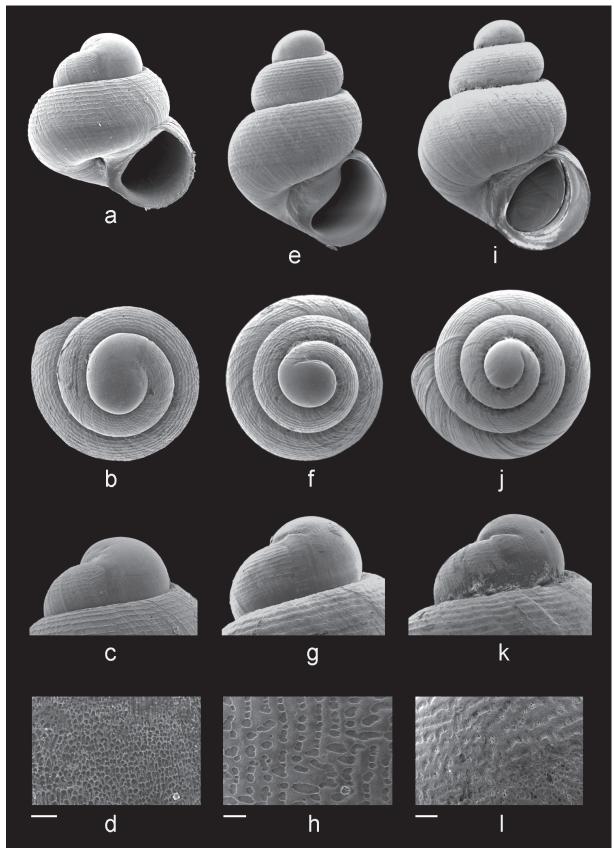


Fig. 84, a–d. *Georissa leucococca* Vermeulen, Liew & Schilthuizen, 2015, a. frontal view, shell 0.7 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa nephrostoma* Vermeulen, Liew & Schilthuizen, 2015, e. frontal view, shell 1.2 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa xesta* F G Thompson & Dance, 1983, i. frontal view, shell 1.2 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: 10 µm.

Cross diagnosis. Uniquely identified among Sabah Georissa by the distinctly convex, inflated parietal peristome.

Description. Shell minute, solid, approx. opaque, red to brown. Surface dull. Spire conical with rounded apex, last whorl slightly turned inwards or not. Whorls convex, evenly rounded, slightly shouldered below the suture. Sculpture. Protoconch with partly aligned, shallow, circular or elliptic depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 12–14 rather densely placed and rather evenly spaced, distinctly but finely wavy, low, flat spiral threads on the first teleoconch whorl; at the start of the last whorl the threads are still present, with some neighboring threads wavy in opposite direction and therefore meeting at intervals, causing a sculpture of aligned depressions; on the last half-whorl more threads meet while fading at the same time; basal area with fine threads fading towards the aperture. Aperture reniform, parietal side distinctly convex and inflated. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 0.87–1.24 mm; width 0.69–0.92 mm; ratio height/width 1.26–1.43; number of whorls 2 3/4–3; height aperture 0.40–0.55 mm; width aperture 0.43–0.60 mm; ratio height/width aperture 0.92–0.95.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. Primary forest, secondary forest. Endemic to Sabah.

Georissa xesta F G Thompson & Dance, 1983

(fig. 84i–l, map 16b)

Thompson & Dance 1983: 125; Khalik et al. 2019: 74. - Type from Malaysia, Sabah, Kudat.

Georissa williamsi auct. Saul 1967: 109.

Georissa bangueyensis auct. Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41.

Georissa sp. 'bo-02' Schilthuizen & Vermeulen 2003a: 95.

[Not Georissa williamsi Godwin-Austen].

[Not Georissa bangueyensis E A Smith].

Cross diagnosis. Differs from *Georissa bangueyensis* by the denser and finer spiral sculpture: 15–25 threads measured at the start of the ultimate whorl above the periphery, versus 8–12 threads. Also, *G. xesta* has, on average, a wider conical shell.

Description. Shell minute, solid, approx. opaque, orange-red. Surface dull or slightly shiny. Spire conical with somewhat narrowly rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, not or hardly shouldered below the suture. Sculpture. Protoconch with partly concatenated shallow depressions or rugulose (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 15–25 rather densely placed and evenly spaced, straight, low, thin spiral threads on the first teleoconch whorl; at the end of the penultimate whorl the threads are still present, though often more prominent above the periphery, but on the last half-whorl most or all have faded; basal area with traces of fine threads near the parietal peristome only. Aperture approx. semi-elliptic, parietal side approx. straight to slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.10–1.68 mm; width 0.84–1.18 mm; ratio height/width 1.22–1.45; number of whorls 2 3/4–3; height aperture 0.48–0.66 mm; width aperture 0.50–0.74 mm; ratio height/width aperture 0.84–0.98.

Distribution in Sabah. Rather common in E; elsewhere in Kudat only. 0–300 m. Primary forest, secondary forest and coastal vegetation on limestone bedrock. Endemic to Sabah.

Group 6

Check also:

Georissa xesta (Group 3). Large shells overlap in shell height with *G. williamsi* but hardly so in shell width (0.84–1.18 mm in the former, 1.10–1.42 mm in the latter): The last whorl increases more slowly in diameter. Also, *G. xesta* largely lacks spiral sculpture on the last half-whorl.

Georissa filiasaulae (Group 1). Relatively smooth shells resemble *G. williamsi* but differ by the white color and by the presence of a shoulder, just below the suture, with minute knobs or scales.

Georissa gomantonensis E A Smith, 1893

(fig. 85a–d, map 16c)

Smith 1893b: 351; Von Martens 1908: 259; Thompson & Dance 1983: 121; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Khalik et al. 2019: 64. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

[Not Hydrocena gomantongensis auct. Solem 1964: 8; = Georissa similis E A Smith].

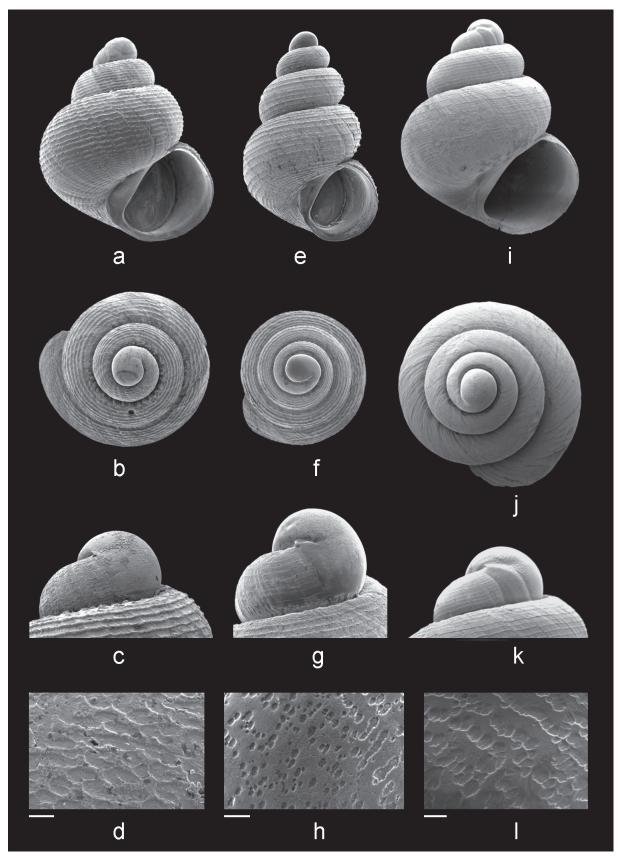


Fig. 85, a–d. *Georissa gomantonensis* E A Smith, 1893, a. frontal view, shell 1.9 mm high, b. apical view, c. apex, d. sculpture apex; e–h. *Georissa insulae* Khalik et al., 2019, e. frontal view, shell 2.0 mm high, f. apical view, g. apex, h. sculpture apex; i–l. *Georissa williamsi* Godwin-Austen, 1889, i. frontal view, shell 1.8 mm high, j. apical view, k. apex, l. sculpture apex. Scale bars d, h, l: $10 \mu m$.

Cross diagnosis. Within Group 6, it shares the fine but distinct spiral sculpture with Georissa insulae, but it differs by its wider shell: Shell width 1.67–1.68 mm and ratio height/width 1.17–1.29, versus shell width 1.21–1.40 mm and ratio height/width 1.42–1.51.

Description. Shell very small, solid, slightly translucent to opaque, green-ochre. Surface dull. Spire conical with narrowly rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, narrowly shouldered just below the suture. Sculpture. Protoconch densely rugulose with partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines some of which develop into a small knob or crest over the shoulder. Spiral sculpture: 14–18 moderately and rather evenly spaced, rather distinct, somewhat wavy, low, narrow spiral threads on the first teleoconch whorl which continue all the way to the aperture; basal area with finer and somewhat more densely placed threads. Aperture approx. semi-elliptic, basal corner obtusely angular, parietal side approx. straight or slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.95–2.17 mm; width 1.67–1.68 mm; ratio height/width 1.17–1.29; number of whorls 3–3 1/4; height aperture 0.94–0.97 mm; width aperture 1.04–1.08 mm; ratio height/width aperture 0.87–0.92.

Distribution in Sabah. Rather common in E; elsewhere in Sapulut only. 0–500 m. Primary and secondary forest on limestone bedrock; observed on vegetation rather than on rocks. Endemic to Sabah.

Georissa insulae Khalik, Hendriks, Vermeulen & Schilthuizen, 2019

(fig. 85e-h, map 15d)

Khalik et al. 2019: 68. – Type from Malaysia, Sabah, Mantanani Besar island . *Georissa williamsi* auct. Clements et al. 2008: 2762; Phung et al. 2017: 68. [Not *Georissa williamsi* Godwin-Austen].

Description. Shell minute to very small, solid, approx. opaque, orange. Surface dull. Spire elevated conical with narrowly rounded apex; last whorl slightly turned inwards. Whorls convex, evenly rounded, not or hardly shouldered. Sculpture. Protoconch with locally clustered, shallow, circular to elliptic depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 10–14 rather widely and somewhat unevenly spaced, distinct, approx. straight, rather high, narrow spiral threads on the first teleoconch whorl which continue all the way to the aperture (with a few more much finer, indistinct spiral threads in between) and locally develop a somewhat nodular crest on the last whorl; basal area with finer and more densely placed threads. Aperture approx. semi-elliptic, parietal side approx. straight or slightly concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.78–2.11 mm; width 1.21–1.40 mm; ratio height/width 1.42–1.51; number of whorls 3–3 1/4; height aperture 0.66–0.79 mm; width aperture 0.74–0.84 mm; ratio height/width aperture 0.89–0.94.

Distribution in Sabah. Scattered localities in N: Mantanani and Malawali islands, Kota Belud, mount Kinabalu. Elevation range: 0–1100 m. In (disturbed) primary forest, coastal woodland. On limestone and sandstone/shale bedrock. Endemic to Sabah.

Georissa williamsi Godwin-Austen, 1889

(fig. 85i–l, map 15e)

Godwin-Austen 1889: 353; Von Martens 1908: 259; Thompson & Dance 1983: 124; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 68; Khalik et al. 2019: 56. – *Hydrocena williamsi* (Godwin-Austen) Saul 1967: 109. – Type from 'Borneo'.

Georissa sp.1. Clements et al. 2008: 2762.

[Not *Georissa williamsi* auct. Clements et al. 2008: 2762; Phung et al. 2017: 68; = *Georissa insulae* Khalik et al.]. [Not *Georissa williamsi* auct. Saul 1967: 109; = *Georissa xesta* F G Thompson & Dance].

Cross diagnosis. Differs from Georissa gomantongensis and G. insulae by its finer and less conspicuous spiral sculpture; from G. gomantongensis it also differs by its narrower shell: Shell width 1.10–1.42 mm versus shell width 1.67–1.68 mm.

Description. Shell minute, solid, slightly translucent to opaque, orange to red. Surface dull or slightly shiny. Spire conical with narrowly rounded apex, last whorl slightly turned inwards. Whorls convex, evenly rounded, not or hardly shouldered. Sculpture. Protoconch densely rugulose with partly concatenated, shallow depressions of uneven shape and size (at 100x magnification). Teleoconch. Radial sculpture subordinate to the spiral sculpture: Unevenly spaced, locally somewhat raised growth lines. Spiral sculpture: 20 or more and rather widely and slightly unevenly spaced, fine and rather inconspicuous, somewhat wavy, low, narrow spiral threads on the first teleoconch whorl which continue all the way to the aperture; basal area with still finer and more densely placed threads. Aperture approx. semi-elliptic, basal corner obtusely angular, parietal side approx. straight or slightly

Subclass: NERITOMORPHA Order: CYCLONERITIDA

concave. Umbilicus closed, umbilical region not or hardly impressed. Dimensions. Height 1.41–1.91 mm; width 1.10–1.42 mm; ratio height/width 1.24–1.38; number of whorls 2 3/4–3 1/4; height aperture 0.60–0.81 mm; width aperture 0.64–0.87 mm; ratio height/width aperture 0.87–0.92.

Distribution in Sabah. Rare in S and E: Sapulut, Baturong-Madai, Batu Tengar. Elevation range: 0–600 m. Primary and secondary forest on limestone bedrock. Endemic to Sabah.

Subclass: HETEROBRANCHIA Order: ELLOBIIDA

Family **ELLOBIIDAE** L Pfeiffer, 1854

Diagnosis for the Sabah species (species from coastal environments excluded). Snails. Shell with 4 3/4–6 slowly expanding whorls. Shell dextral, minute, distinctly higher than wide; spire narrowly ovoid; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines; spiral sculpture very fine. Aperture with teeth. Peristome on the palatal side thickened, spreading. Umbilicus closed. Dimensions: Adults 1.7–2.2 mm high, 0.7–1.0 mm wide.

Note. We include the single fully terrestrial species only. All coastal species from the region are revised in Raven & Vermeulen (2007). We correct one error: *Ellobium tornatelliforme* auct. Vermeulen & Raven (2007: 41) is *E. pallidum* (G B Sowerby II, 1839) (comm. J G M Raven).

Genus Carychium O F Müller, 1773

Carychium diplotylon Vermeulen & Liew, new species

(fig. 86, map 16d)

Type specimens from Malaysia, Sabah, Crocker Range N.P., Mahua falls (holotype BOR/MOL 1790; paratypes JV 9731/50 shells).

Carychium javanum auct. Schilthuizen 2004: 95. [Not Carychium javanum Von Möllendorff].

Description. Shell minute, thin, translucent, white. Surface with a silky luster. Spire narrowly ovoid to conical, apex not or hardly drawn-out, rounded. Whorls convex, suture impressed. Sculpture. Protoconch minutely punctate (just visible at 40x magnification) and with a few spiral striae just below the suture. Teleoconch. Radial sculpture: Top whorls with approx. scattered, unevenly placed, fine, low, rounded riblets, shell surface in between shallowly punctate, later whorls with increasingly densely placed and evenly spaced riblets, not punctate. Spiral sculpture absent. Aperture obliquely ovate, broadly rounded at the base, more narrowly rounded above, with 4



Fig. 86. *Carychium diplotylon* Vermeulen & Liew, new species, frontal view, shell 1.75 mm high.

teeth: 1 distinctly protruding parietal lamella, 1 distinct columellar lamella which in some specimens starts somewhat deeper inside and is therefore inconspicuous if the shell is observed frontally, and 2 palatal knobs, the upper distinct, on the inner peristome, the lower slightly less distinct, just behind the peristome. Peristome double, the outer slightly spreading on the palatal and basal side, the inner forming a thick glazing on the parietal side, elsewhere forming a thick lip. Umbilicus closed. Dimensions. Height 1.55–1.80 mm; width 0.75–0.80 mm; ratio height/width 2.0–2.4; number of whorls 4 3/4–5; height aperture 0.6–0.7 mm; width aperture 0.55–0.60 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 1000–1900 m. Primary and secondary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. 1. Differs from Carychium javanum Von Möllendorff, 1897, C. thailandicum J B Burch & Panha, 1988, and C. indicum Benson, 1849, by the presence of two rather well-demarcated knobs on the palatal side of the aperture (versus one distinct knob, or a slight thickening only). It shares this character with C. javanum elatum Van Benthem Jutting, 1959 but differs by its smaller size (shell 1.55–1.80 mm high and 0.75–0.80 mm wide versus 2.2–2.6 mm high and 0.9–1 mm wide) and by the much thinner peristome, which is more narrowly rounded on the upper side.

Name derivation. From διπλῶς (Ancient Greek) = twice as many, and τύλος = knob.

Subclass: HETEROBRANCHIA Order: STYLOMMATOPHORA

Family **ACHATINELLIDAE** Gulick, 1873

Diagnosis for the Sabah species. Snails. Shell with up to 3 1/2–4 1/2 (rather) slowly expanding whorls. Shell dextral, very small, higher than wide; spire ovoid to conical with convex sides; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines in some species locally raised to fine riblets; spiral sculpture absent or very fine. Aperture with a parietal tooth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed. Dimensions: Adults up to 2.3–3.3 mm high, 1.1–2.0 mm wide.

Note. Revised in Cooke & Kondo (1960).

Genus *Elasmias* Pilsbry, 1910

Diagnosis for the Sabah species. Columellar peristome rather distinctly sigmoid.

Elasmias globulosum Quadras & Von Möllendorff in Zilch, 1962

(fig. 87a, map 16e)

Zilch 1962: 78; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 69. – Type from Philippines, Mindanao.

Cross diagnosis. Differs from *Elasmias manilense* by the wider spire (width of the third whorl c. 1.8 mm, versus 1.0–1.4 mm).

Description. Shell very small, thin, translucent, pale yellowish brown. Surface shiny. Spire (broadly) ovoid. Whorls moderately convex, last whorl rounded, slightly convex below the periphery. Sculpture. Radial sculpture: Inconspicuous growth lines, locally grading into very fine (just visible at 40x magnification), densely placed, low radial riblets, particularly on the top whorls. Spiral sculpture: Very fine (just visible at 40x magnification), densely placed grooves present over most of the shell surface. Aperture with a parietalis which is distinct in juveniles, inconspicuous or almost absent in adults. Peristome on the columellar side flatly but rather distinctly sigmoid, extended over the umbilical area as a thin glazing. Umbilicus closed. Dimensions. Height up to 2.7 mm; width up to 2.0 mm; diameter of the first three whorls c. 0.6 mm, 1.1 mm, 1.8 mm respectively; number of whorls up to 3 1/2; height aperture up to 1.5 mm; width aperture up to 1.2 mm.

Distribution in Sabah. Widespread but rare: Sapulut, lower Kinabatangan. Elevation range: 0–400 m. In (disturbed) primary forest on limestone bedrock. Also in Sarawak. Distribution elsewhere: Philippines (Luzon, Mindanao).

Elasmias manilense (Dohrn, 1863)

(fig. 87b–d, map 16e)

Pilsbry 1915 (1914–1916): 125; Van Benthem Jutting 1952: 346; 1959: 124; Cooke & Kondo 1960: 225; Zilch 1962: 79; Solem 1988: 469; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 70. – *Tornatellina manilensis* Dohrn 1863: 160; Pfeiffer & Clessin 1881: 342. – Type from Philippines, Luzon, near Manila.

Description. Shell very small, thin, translucent, pale yellowish brown. Surface shiny. Spire rather narrowly ovoid. Sculpture. Radial sculpture: A few inconspicuous growth lines. Spiral sculpture: Very fine (just visible at 40x magnification), densely placed grooves present on the first teleoconch whorls. Aperture with a parietalis which is distinct in juveniles, more inconspicuous in adults. Peristome on the columellar side (flatly) and (rather) distinctly sigmoid, extended over the umbilical area as a thin glazing. Umbilicus closed. Dimensions. Height up to 3.3 mm; width up to 1.6 mm; diameter of the first three whorls 0.4–0.5 mm, 0.7–0.9 mm, 1.0–1.4 mm respectively; number of whorls up to 4 1/2; height aperture up to 1.35 mm; width aperture up to 1.1 mm.

Distribution in Sabah. Scattered localities in coastal areas and on islands: Labuan Marine Park, Mantanani islands, Balambangan island, Tun Sakaran Marine Park. Elevation range: 0–200 m. Coastal woodland on limestone bedrock. Distribution elsewhere: India (Maldives), Vietnam (N part), Indonesia (Natuna islands, Java, West Papua), Philippines.

Variability. The shell width is slightly variable, see the width of the third whorl.

Genus Tornatellinops Pilsbry & C M Cooke, 1915

Diagnosis for the Sabah species. Columellar peristome almost straight.

Tornatellinops moluccanus (O Boettger, 1891)

(fig. 87e, map 16f)

Pilsbry 1915 (1914–1916): 186; Cooke & Kondo 1960: 170; Zilch 1962: 80; Phung et al. 2017: 70. – *Tornatellina moluccana* Boettger 1891: 274. – Type from Indonesia, Moluccas, Ambon

Description. Shell very small, thin, translucent, pale yellowish brown. Surface shiny. Spire narrowly ovoid. Sculpture. Radial sculpture: A few inconspicuous growth lines. Spiral sculpture absent, or a few traces of a very fine striation (just visible at 40x magnification) on the protoconch only. Aperture with a distinct parietalis. Peristome on the columellar side hardly sigmoid, forming a low ridge bordering the aperture, not extending over the umbilical area. Umbilicus closed. Dimensions. Height up to 2.3 mm; width up to 1.1 mm; diameter of the first three whorls 0.3–0.35 mm, 0.6–0.65 mm, c. 0.8 mm respectively; number of whorls up to 4 1/2; height aperture up to 0.9 mm; width aperture up to 0.6 mm.

Distribution in Sabah. Scattered localities in coastal areas and on islands: Labuan Marine Park, W Coast islands, Semporna peninsula. Elevation range: 0–400 m. In secondary woodland on volcanic bedrock. Distribution elsewhere: Indonesia (Maluku).

Family ACHATINIDAE Swainson, 1840

(Incl. SUBULINIDAE P Fischer & Crosse, 1877)

Diagnosis for the Sabah species. Snails. Shell with up to 9 slowly expanding whorls. Shell dextral, small to medium-sized (very large in Lissachatina), higher than wide; spire (elongated) conical to subcylindrical; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth lines locally raised to riblets, or of fine, dense radial riblets (widely spaced, narrow but deep grooves in Curvella hadrotes), spiral sculpture approx. absent (inconspicuous in Lissachatina). Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed. Dimensions: Adults up to 6.5–20 mm high, 1.4–5.0 mm wide (up to 170 mm high, 60 mm wide in Lissachatina).

Notes. 1. *Cecilioides* (Ferussaciidae) resembles small to medium-sized Achatinidae; differences are given under Ferussaciidae.

2. First we describe the large and conspicuous *Lissachatina*, then the genera with small, similar-looking shells.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Shell up to 170 mm high, 60 mm wide, white with brown color pattern
- Genus Lissachatina

- 1 Shell up to 6.5–20 mm high, 1.4–5.0 mm wide, white
 - 2 Teleoconch with widely spaced, narrow and rather deep radial grooves, with fine radial striation in between Genus *Curvella*
 - 2 Teleoconch without or (locally) with densely placed, fine radial riblets
 - 3 Peristome distinctly sinuous on the columellar side. Growth lines hardly curved Genus *Subulina*
 - 3 Peristome straight or slightly sinuous on the columellar side. Growth lines curved
 - 4 Spire slightly pinched around the second to the fourth whorl; the apex appears slightly drawn-out as a result Genus *Paropeas*
 - 4 Spire evenly expanding; apex not drawn-out
 - 5 Protoconch with traces of minute radial striation, particularly below the suture. Outer whorls usually with a slight subsutural furrow Genus *Opeas*
 - 5 Protoconch smooth. Outer whorls without subsutural furrow

Genus Allopeas

Genus Lissachatina Bequaert, 1950

Diagnosis for the Sabah species. Shell very large, white with brown color pattern. Apex not drawn-out. Whorls without a subsutural furrow. Protoconch smooth. Radial sculpture on teleoconch: Weak growth lines to rather distinct, (moderately) curved, dense riblets. Peristome sinuous on the columellar side.

Lissachatina fulica (Bowdich, 1822)

(fig. 88, 90a, map 17a)

Inkhavilay et al. 2019: 49. – Achatina fulica Bowdich, 1822: Pl. 13 fig. 3; Van Benthem Jutting 1952: 391; 1959:

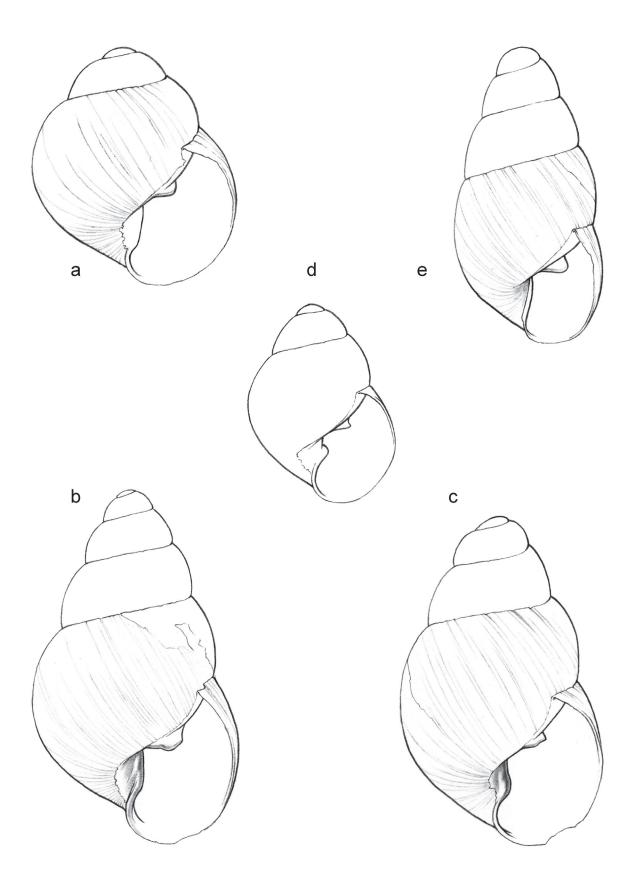


Fig. 87, a. *Elasmias globulosum* Quadras & Möllendorff ex Zilch, 1962, frontal view, shell 2.0 mm high; b–d. *Elasmias manilense* (Dohrn, 1863), frontal views, b. Shell 2.9 mm high, c. Shell 2.7 mm high, d. Juvenile, shell 1.4 mm high; e. *Tornatellinops moluccanus* (O Boettger, 1891), frontal view, shell 2.3 mm high.

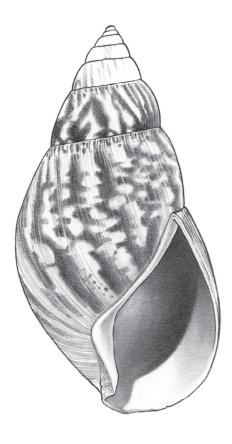


Fig. 88. *Lissachatina fulica* (Bowdich, 1822), frontal view, shell 100 mm high.

134; Cowie 1997: 15; Vermeulen & Whitten 1998: 90, 148; Schilthuizen & Rutjes 2001: 420; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 52, 53; Phung et al. 2017: 71; Marzuki et al. 2021: 44. – Achatina (Achatinus) fulica (Bowdich) Pfeiffer 1855b: 168. – Achatina (Lissachatina) fulica (Bowdich) Fontanilla 2010: 1. – Type from Bourbon.

Helix (Cochlitoma) fulica, unavailable name, Férussac 1821 (1821–1822): Limaçons 49.

Description. Shell very large, solid, opaque, offwhite with brown blotches which approx. follow the growth lines or are arranged in a zig-zag pattern. Surface somewhat shiny. Spire conical with about straight sides. Whorls moderately convex, last whorl rounded, slightly convex below the periphery. Sculpture. Radial sculpture: Growth lines grading into inconspicuous radial riblets, most conspicuous just below the suture. Spiral sculpture: Traces of striation, most conspicuous below the suture. Aperture inside white or pale blueish, brownish close to the peristome. Peristome not spreading on palatal and basal side, extended over the parietal and columellar side as a thin glazing. Umbilicus closed. Dimensions. Height up to 100(-170) mm; width up to 45(-60) mm; number of whorls up to 7(-9); height aperture up to 47 mm; width aperture up to 30 mm. Periostracum yellowish brown.

Distribution in Sabah. Widespread, common, under-recorded. Elevation range: 0–800 m. In recently disturbed primary forest, secondary woodland, plantations, gardens, grass lands, around human settlements. Also in Brunei, Sarawak, Kalimantan. Introduced, an agricultur-

al pest. Distribution elsewhere: Widespread in (seasonally) humid tropics. Natural range: Africa.

Notes. 1. Elsewhere in decline after introduction and initial explosion of the population. No decline has been observed yet in Borneo.

2. The snail serves as intermediate host of the rat lungworm *Angiostrongylus cantonensis* (Chen, 1935). The third juvenile stage of this accidentally infects humans, who, after ingestion, may develop *Eosinophilic meningo-encephalitis* (EME) or *Angiostrongyliasis*, a disease of the central nervous system; see Fontanilla (2010).

Genus Allopeas H B Baker, 1935

(= Lamellaxis auct.)

Diagnosis for the Sabah species. Shell small to medium-sized, white. Apex not drawn-out. Whorls without a subsutural furrow. Protoconch smooth. Radial sculpture on teleoconch: Weak growth lines to rather distinct, (moderately) curved, dense riblets. Peristome slightly sinuous on the columellar side.

Allopeas clavulinum (Potiez & Michaud, 1838)

fig. 89c-d, map 17b)

Cowie 1997: 34; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Phung et al. 2017: 93; Marzuki et al. 2021: 45. – Bulimus clavulinus Potiez & Michaud 1838: 136. – Bulimus (Opeas) clavulinus (Potiez & Michaud) Pfeiffer 1855b: 155. – Stenogyra (Opeas) clavulina (Potiez & Michaud) Pfeiffer & Clessin 1881: 321. – Opeas clavulinum (Potiez & Michaud) Boettger 1891: 272; Pilsbry 1906 (1906–1907): 135; Van Benthem Jutting 1952: 381. – Lamellaxis clavulinus (Potiez & Michaud) Van Benthem Jutting 1958a: 106; 1958b 327; 1959: 131; Saul 1967: 109; Solem 1988: 523; Maassen 1997: 53; Vermeulen & Whitten 1998: 86, 147; Maassen 2001: 83; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42. – Type from Reunion.

Cross diagnosis. Resembles *Allopeas gracile*, differs by the wider shell (width of the fourth whorl 2.1–2.8 mm, versus 1.4–1.8 mm). Also, the radial sculpture is usually less conspicuous.

Description. Shell small to medium-sized, thin, slightly translucent, white or yellowish corneous. Surface shiny. Spire elongated-conical with slightly convex sides, apex not drawn-out. Whorls convex, without subsutural furrow; suture moderately impressed. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak to rather distinct, (moderately) curved growth lines, often developing into weak, somewhat uneven, rather densely placed, low riblets. Spiral sculpture absent. Aperture obliquely elliptic, peristome not thickened nor spreading, columellar side only slightly sinuous. Umbilicus closed. Dimensions. Height up to 13.5 mm (the first 4 whorls 2.5–3.3 mm); width up to 4.5 mm (the second whorl 1.1–1.3 mm; the fourth whorl 2.1–2.8 mm); number of whorls up to 8 1/2, height aperture up to 4.7 mm; width aperture up to 3 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. Primary and secondary forest. Introduced. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: Africa, Asia, Australia, Pacific. Natural range: Probably E Africa.

Note. The status of this, next to *Allopeas gracile*, is unresolved, see Solem (1988). A slight morphological overlap exists between the two.

Allopeas gracile (T Hutton, 1834)

(fig. 89a-b, map 17c)

Cowie 1997: 34; Maassen 2001: 81; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54; Phung et al. 2017: 91; Marzuki et al. 2021: 46. – Bulimus gracilis Hutton 1834: 84, 93. – Bulimus (Opeas) gracilis (T Hutton) Pfeiffer 1855b: 156. – Stenogyra gracilis (T Hutton) Von Martens 1867: 375; Issel 1874: 414; Tenison Woods 1888: 1051. – Stenogyra (Opeas) gracilis (T Hutton) Pfeiffer & Clessin 1881: 321. – Opeas gracile (T Hutton) Boettger 1891: 272; Von Möllendorff 1894: 211; Pilsbry 1906 (1906–1907): 125; Von Martens 1908: 262; Van Benthem Jutting 1952: 378. – Lamellaxis gracilis (T Hutton) Van Benthem Jutting 1958a: 106; 1958b 327; 1959: 131; Saul 1967: 109; Solem 1988: 521; Maassen 1997: 53; Vermeulen & Whitten 1998: 86, 147; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Tan et al. 2012: 99. – Type from India, 'Mirzapoor'.

Paropeas achatinaceum auct. Schilthuizen & Vermeulen 2003a: 96. [Not Paropeas achatinaceum (L Pfeiffer)].

Cross diagnosis. Shells with a conspicuous sculpture resemble *Opeas hannense* but grow larger (shell height up to 15.2 mm, versus 6.5 mm), and do not have a subsutural furrow. Such shells also resemble *Paropeas achatinaceum*, but do not have the slightly drawn-out apex and are shinier.

Description. Shell small to medium-sized, thin, slightly translucent, white or yellowish corneous. Surface shiny. Spire elongated-conical with approx. straight sides, apex not drawn-out. Whorls convex, without subsutural furrow; suture moderately impressed. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak to distinct, (moderately) curved growth lines, sometimes developing into rather distinct, somewhat uneven, rather densely placed, low riblets. Spiral sculpture absent. Aperture obliquely elliptic, peristome not thickened nor spreading, columellar side only slightly sinuous. Umbilicus closed. Dimensions. Height up to 15.2 mm (the first 4 whorls 2–3 mm); width up to 3.6 mm (the second whorl 0.8–1.1 mm; the fourth whorl 1.4–1.8 mm); number of whorls up to 9, height aperture up to 3.8 mm; width aperture up to 2.2 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2000 m. In secondary forest, coastal vegetation, agricultural land. Sometimes in large numbers in and around caves inhabited by bats or swiftlets, in the periphery of minor guano deposits but well away from large guano accumulations. Introduced. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: Circumtropical. Natural range: Probably Neotropics.

Genus Curvella Chaper, 1885

Diagnosis for the Sabah species. Shell small, white. Apex not drawn-out. Whorls without a subsutural furrow. Protoconch smooth. Radial sculpture on teleoconch: Widely spaced, curved, rather fine but narrow and rather deep grooves. Peristome evenly rounded on the columellar side.

Curvella hadrotes Vermeulen, Liew & Schilthuizen, 2015

(fig. 89e-f, map 17d)

Vermeulen et al. 2015: 111. – Type from Malaysia, Sabah, Tawau Prov., Danum valley Conservation Area, 2 km NW of Research Station.

'Borneopeas' sp. 1 Clements et al. 2008: 2762.

Prosopeas 'sp. bo-01' Schilthuizen & Vermeulen 2003a: 96.

Cross diagnosis. Among Achatinidae with small shells from Borneo identified by its small subcylindrical shell and the widely spaced, narrow radial grooves.

Description. Shell small, thin, slightly translucent, white. Surface glossy. Spire subcylindrical, only slightly tapering towards the apex, with slightly convex sides. Whorls: Apical whorls moderately convex, others slightly convex, without subsutural furrow, the last whorl slightly flattened around the periphery; suture moderately impressed. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture predominant, widely and somewhat unevenly spaced, curved, rather fine but narrow and rather deep grooves, in between these finer, inconspicuous striation present locally. Spiral sculpture: Absent or a very fine spiral striation particularly present locally on the apical whorls, shallowly engraved in the areas in between the radial grooves. Aperture oblique, narrowly ovate, peristome not thickened nor spreading, columellar side evenly rounded. Umbilicus closed. Dimensions. Height 7.5–7.8 mm; width 1.4–1.5 mm; number of whorls c. 6 1/8, height aperture 2.8–3.0 mm; width aperture 1.4–1.5 mm.

Distribution in Sabah. Rare in S and E: Sapulut, Danum valley, Ulu Segama, Tabin. Elevation range: 0–400 m. In primary and secondary forest on limestone bedrock. Endemic to Sabah.

Genus Opeas Albers, 1850

Diagnosis for the Sabah species. Shell small, white. Apex not drawn-out. Outer whorls with a slight subsutural furrow. Protoconch with traces of minute radial striation, particularly below the suture. Radial sculpture on teleoconch: Conspicuous, fine, somewhat uneven, rather densely placed, curved radial riblets. Peristome approx. straight on the columellar side.

Opeas hannense (Rang, 1831)

(fig. 89h, map 17e)

Pilsbry 1906 (1906–1907): 141; Cowie 1997: 36; Clements et al. 2008: 2762. – Helix (Cochlicella) hannensis Rang 1831: 41. – Stenogyra (Opeas) hannensis (Rang) Pfeiffer & Clessin 1881: 322. – Type from Cape Verde. Bulimus pumilus Pfeiffer 1840: 252. – Opeas pumilum (L Pfeiffer) Pilsbry 1946: 181; Solem 1988: 524; Maassen 2001: 79; Tan et al. 2012: 100. – Type from Cuba.

Stenogyra didyma Westerlund 1883: 51. – Opeas didyma Marzuki et al. 2021: 46. – Type from Singapore.

Cross diagnosis. The distinct radial sculpture is reminiscent of *Paropeas achatinaceum*, but *Opeas hannense* is smaller (width second whorl 0.7–0.9 mm, width fourth whorl 1.2–1.5 mm, versus 1–1.2 mm, 1.7–2.3 mm). Also, it usually differs by the presence of a slight subsutural furrow.

Description. Shell small, thin, translucent to opaque, white to pale corneous. Surface shiny. Spire elongated-conical with approx. straight sides, apex not drawn-out. Whorls moderately convex; later whorls usually with a slight furrow immediately below the suture, suture shallow. Sculpture. Protoconch with traces of minute radial striation, particularly below the suture. Teleoconch. Radial sculpture: Conspicuous, fine, somewhat uneven, rather densely placed, curved radial riblets. Spiral sculpture absent. Aperture obliquely elliptic, peristome not thickened nor spreading, columellar side approx. straight. Umbilicus closed. Dimensions. Height up to 6.5 mm (the first 4 whorls 2.0–2.5 mm); width up to 2.1 mm (the second whorl 0.7–0.9 mm; the fourth whorl 1.2–1.5 mm); number of whorls up to 6 1/8, height aperture up to 2 mm; width aperture up to 1.1 mm.

Distribution in Sabah. Rare in E: Selingan island, lower Kinabatangan, Semporna Peninsula. Elevation range: 0–100 m. Disturbed primary and secondary forest, also in plantations; on limestone bedrock. Introduced. Also in Sarawak, Kalimantan. Distribution elsewhere: Malaysia (Peninsula) and Singapore to New Guinea, Pacific, central and S America, Cape Verde islands. In temperate climates in greenhouses. Natural range: central and S America.

Notes. 1. Probably recently introduced into Borneo. Extensive collecting in 1985/86 and in 1990 did not yield a single specimen of *Opeas hannense*, whereas it was found in ten different localities throughout Borneo in 2002/04.

2. Cowie (1997) has been followed for synonymy.

Genus Paropeas Pilsbry, 1906

(= Prosopeas auct.)

Diagnosis for the Sabah species. Shell small to medium-sized, white. Apex slightly drawn-out. Whorls without a subsutural furrow. Protoconch smooth, often with fine radial riblets just below the suture. Radial sculpture on teleoconch: Distinct, fine, somewhat uneven, densely placed, curved radial riblets. Peristome approx. straight on the columellar side.

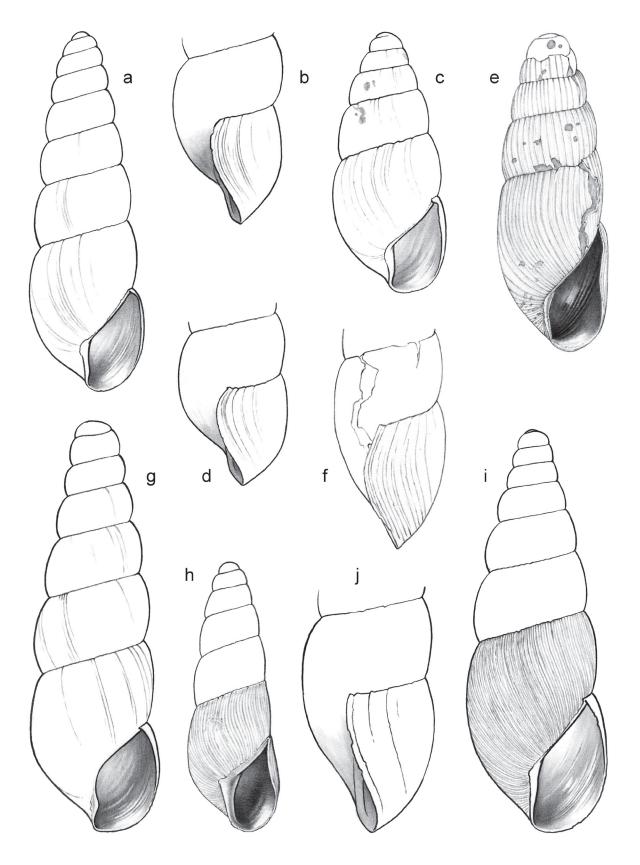


Fig. 89, a–b. *Allopeas gracilis* (T Hutton, 1834), a. Frontal view, shell 9.3 mm high, b. Right lateral view; c–d. *Allopeas clavulinum* (Potiez & Michaud, 1838), c. Frontal view, shell 6.7 mm high, d. Right lateral view; e–f. *Curvella hadrotes* Vermeulen, Liew & Schilthuizen, 2015, e. Frontal view, shell 7.8 mm high, f. Right lateral view; g. *Subulina octona* (Bruguière, 1789), frontal view, shell 12 mm high; h. *Opeas hannense* (Rang, 1831), frontal view, shell 6 mm high; i–j. *Paropeas achatinaceum* (L Pfeiffer, 1846), i. Frontal view, shell 11.6 mm high, j. Right lateral view.

Paropeas achatinaceum (L Pfeiffer, 1846)

(fig. 89i-j, map 17f)

Naggs 1994: 176; Cowie 1997: 37; Vermeulen & Whitten 1998: 88, 147; Naggs & Raheem 1999: vii, 96; Maassen 2001: 80; Schilthuizen & Rutjes 2001: 420; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Phung et al. 2017: 90; Foon et al. 2018: 96; Marzuki et al. 2021: 48. – Bulimus achatinaceus Pfeiffer 1846b: 82; 1848b: 156. – Bulimus (Opeas) achatinaceus (L Pfeiffer) Pfeiffer 1855b: 155. – Opeas achatinaceum (L Pfeiffer) Wallace 1865: 413; Von Martens 1908: 262. – Stenogyra achatinacea (L Pfeiffer) Von Martens 1867: 375; Issel 1874: 414; Tenison Woods 1888: 1052. – Stenogyra (Opeas) achatinacea (L Pfeiffer) Pfeiffer & Clessin 1881: 320. – Prosopeas achatinaceum (L Pfeiffer) Pilsbry 1906 (1906–1907): 21; Van Benthem Jutting 1952: 385; 1959: 132; Solem 1988: 524; Maassen 1997: 54. – Type from Indonesia, Java.

[Not Prosopeas achatinaceum auct. Schilthuizen et al. 2003a: 96; = Allopeas gracile (T Hutton)].

Cross diagnosis. Differs from Opeas and Allopeas by the slightly tapering spire; the apex appears slightly drawn-out. It also differs from Allopeas by the somewhat dull appearance caused by the dense, distinct radial sculpture (Allopeas has a shinier shell with, generally, less distinct radial sculpture). It also differs from Opeas by its larger size (width second whorl 1–1.2 mm, width fourth whorl 1.7–2.3 mm, versus 0.7–0.9 mm, 1.2–1.5 mm) and by the absence of a slight subsutural furrow.

Description. Shell medium-sized, thin, slightly translucent or opaque, white to pale corneous. Surface dull or slightly shiny. Spire elongated-conical with slightly convex sides, but apical part slightly drawn-out. Whorls moderately convex, without subsutural furrow; suture moderately impressed. Sculpture. Protoconch smooth, often with fine radial riblets just below the suture. Teleoconch. Radial sculpture: Conspicuous, fine, somewhat uneven, densely placed, curved radial riblets. Spiral sculpture: Absent, in some shells present as a fine crenulation locally in the crest of the radial riblets. Aperture obliquely elliptic, peristome not thickened nor spreading, columellar side approx. straight. Umbilicus closed. Dimensions. Height up to 14 mm (the first 4 whorls 2.0–2.5 mm); width up to 4.4 mm (the second whorl 1–1.2 mm; the fourth whorl 1.7–2.3 mm); number of whorls up to 9, height aperture up to 4 mm; width aperture up to 2 mm. Periostracum thin, often folded into a slight crest over each radial riblet.

Distribution in Sabah. Widespread, common. Elevation range: 0–1600 m. In degraded vegetation, in coastal vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Mascarenes, Sri Lanka, SE Asia, Pacific. Natural range: Possibly SE Asia.

Variability. The relative width of the shell varies: Wide shells approach *Allopeas clavulinum* in general outline, narrow shells approach *A. gracile*.

Note. Solem (1988: 524) observes that *Paropeas achatinaceum* seems to displace *Allopeas gracile* after introduction. In Sabah, it seems to be spreading, with only five records before 2002 despite extensive collecting.

Genus Subulina H Beck, 1837

Diagnosis for the Sabah species. Shell small to medium-sized, white. Apex often slightly drawn-out. Whorls without a subsutural furrow. Protoconch smooth. Radial sculpture: Weak, hardly curved growth lines locally. Peristome distinctly sinuous on the columellar side.

Subulina octona (Bruguière, 1789)

(fig. 89g, map 18a)

Boettger 1890: 147; Van Benthem Jutting 1952: 376; 1959: 130; Saul 1967: 110; Solem 1988: 521; Vermeulen 1996b: 289; Cowie 1997: 37; Maassen 1997: 54; Vermeulen & Whitten 1998: 86, 147; Maassen 2001: 82; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Tan et al. 2012: 98; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54; Phung et al. 2017: 93. – Bulimus octonus Bruguière 1789: 325. – Achatina (Subulina) octona (Bruguière) Pfeiffer 1855b: 169. – Stenogyra (Subulina) octona (Bruguière) Pfeiffer & Clessin 1881: 326. – Type from 'Antilles, Guadelupe, Saint-Domingue'

Cross diagnosis. Among Achatinidae with small shells from Sabah identified by the distinctly sinuous columellar side of the peristome.

Description. Shell medium-sized, thin, translucent, white to brownish or greenish corneous. Surface shiny. Spire subcylindrical, only slightly tapering towards the apex but apex itself often slightly drawn-out, sides slightly convex. Whorls convex, without subsutural furrow; suture moderately impressed, often somewhat crenulated. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak, hardly curved growth lines locally, more prominent just below the suture only. Spiral sculpture absent. Aperture obliquely elliptic, peristome not thickened nor spreading, columellar side distinctly sinuous. Umbilicus closed. Dimensions. Height up to 20 mm (the first 4





Fig. 90, a. Lissachatina fulica (Bowdich, 1822); b. Deroceras c.f. laeve (O F Müller, 1774).

whorls 3.8–4.6 mm); width up to 5 mm (the second whorl 1.6–1.9 mm; the fourth whorl 2.2–2.8 mm); number of whorls up to 10, height aperture up to 4.5 mm; width aperture up to 2.8 mm.

Distribution in Sabah. Widespread, common, but rare deep inland (Sapulut). Elevation range: 0–400 m. In degraded woodland, fallow fields, agricultural land, gardens, urban areas, waste land. Introduced. Also in Sarawak, Kalimantan. Distribution elsewhere: Circumtropical. Natural range: Neotropics.

Note. An agricultural pest.

Family AGRIOLIMACIDAE H Wagner, 1935

Diagnosis for the Sabah species. Slugs with a small internal shell situated deep inside the body. Shell shield-shaped, without whorls, apex close to the edge.

Animal sub-circular in section, not flattened, posterior end dorsally keeled. No caudal horn. Mantle anterior, covering up to approx. 1/2 of the length of the dorsal side of the animal when creeping, not covering the head or the sides, not fused to the body (the edges can be lifted), surface with fine, approx. concentric wrinkles. Ventral side undivided, but foot divided into three zones of the same color, separated by grooves. Anus and respiratory pore on the right side, close to the posterior end of the mantle, in a deep sinus in the mantle.

Genus *Deroceras* Rafinesque, 1820

Deroceras laeve (O F Müller, 1774)

(fig. 90b, map 18b)

Van Benthem Jutting 1952: 432; Cowie 1997: 22; Wiktor 2000: 462; Wiktor et al. 2000: 31; Schilthuizen & Liew 2008: 299. – *Limax laevis* Müller 1774: 1. – Type from Denmark.

Description. Shell white, with a calcareous layer and a thick periostracum, shield-shaped, asymmetrically ovate, slightly convex dorsally, slightly concave ventrally.

Animal small, very soft, when creeping approx. cylindrical, with the posterior half often slightly widened and distally rather abruptly narrowed; tail keeled towards the apex. Posterior edge of the mantle approx. half-way the length of the body, surface with distinct, partly concentric wrinkles, but smooth around the anal/respiratory pore. Body including tentacles slightly translucent, grey, yellow-brown to dark brown, with a pale ring around the anal/respiratory pore. Dimensions. Creeping animals up to 25 mm long, up to 4.5 mm wide.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 1500–2000 m. Lawns, gardens and degraded vegetation in area with high rainfall. Introduced, elsewhere an agricultural pest. Distribution elsewhere: Widespread but localized in humid tropics. Natural range: Holarctic.

Notes. 1. Description adapted from Wiktor (2000), Wiktor et al (2000a), Schilthuizen et al. (2008).

2. The identity of the Sabah material has not been anatomically checked.

Family ARIOPHANTIDAE Godwin-Austen, 1883

Diagnosis for the Sabah species. Snails. Shell with up to 3 7/8–6 1/4 slowly expanding whorls, or semi-slugs with the shell partly or entirely covered by the mantle and with up to 3 3/4 rapidly expanding whorls. Shell in snail species dextral, minute to very large, wider than high; spire depressed ovoid to depressed conical to (discoid)lenticular; last whorl rounded to acutely keeled at the periphery; shell in semi-slug species shield-shaped. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines in most species, of very fine, dense radial riblets in some (an uneven sculpture including small wrinkles and dents above the periphery in *Hemiplecta*); spiral sculpture absent or fine. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed or open, narrow. Dimensions: Adults up to 1.1–28.3 mm high, 1.7–51 mm wide.

Animal. Mantle lobes: One or more present, finger-shaped.

Anatomy. Penial structure: Vas deferens attached laterally to the epiphallus. Epiphallus with flagellum. Dart sac without apical glands.

Notes. 1. On family level, Sabah ariophantid shells are indistinguishable from those of Dyakiidae. Usually, the genera are sufficiently distinct, but the shells of ariophantid genera *Macrochlamys* and *Vitrinula* on the one hand, and of the dyakiid genus *Everettia* on the other, are very similar; see the notes with the generic diagnosis of these genera.

2. First, the snail genera a grouped together, then follow the semi-slug genera.

The snails (Animal fully retractable in its shell. Shell not or only for a small part covered by the animal when creeping)

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Shell above the periphery dull or with a silky luster, and with an uneven sculpture including minute wrinkles and dents

 Genus *Hemiplecta*
- 1 Shell above the periphery shiny or glossy, with or without an even sculpture, but without wrinkles and dents
 - 2 Shell width up to 3.6 mm (at $4 \frac{1}{2}$ 5 whorls)

Genus Microcystina

- 2 Shell width 4.2 mm or more (at approx. 3 3/4–4 1/2 whorl)
 - 3 Shell corneous with only a very thin layer of calcareous matter on the inside (shell dents easily)

Genus Durgella

- 3 Shell with a thick calcareous layer
 - 4 Diameter of third whorl 6.1–11 mm; if diameter of third whorl 6.1–7.0 mm then shell with distinct spiral color bands

 Genus *Vitrinula*
 - 4 Diameter of third whorl 2.1–6.5 mm; shell without distinct spiral color bands

Genus Macrochlamys

Genus *Durgella* W T Blanford, 1863

Diagnosis for the Sabah species. Shell corneous with only a very thin layer of calcareous matter on the inside (shell dents easily), without colored bands. Shell shiny, with a fine and even spiral sculpture above the periphery. Shell width in adults of c. 3 3/4 whorls c. 6.2 mm; ratio height/width 0.8–0.9. Umbilicus open, narrow, without spur protruding from the columellar corner.

Note. Genus placed in Helicarionidae in MolluscaBase (accessed 1/2021).

'Durgella' densestriata Vermeulen, Liew & Schilthuizen, 2015

(fig. 91a-c, 96a, map 18c)

Vermeulen et al. 2015: 36. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., summit trail, near Layang-layang at 2641 m.

Durgella sp. Liew et al. 2010: Online Supporting Information, Appendix S1.

Description. Shell small, corneous with only a thin calcareous layer on the inside, somewhat translucent, greenish or brownish. Surface shiny. Outline low-conical with slightly concave sides, apex narrowly rounded. Whorls convex, rounded, suture impressed. Sculpture. Protoconch approx. smooth. Teleoconch. Radial sculpture: unevenly spaced, somewhat raised growth lines, locally grading into some very fine, inconspicuous, densely placed riblets. Spiral sculpture: Above the periphery with distinct, very fine, wavy, densely placed, shallow grooves. Aperture: Peristome not spreading. Umbilicus closed. Dimensions. Height up to 5.5 mm; width up to 6.2 mm; ratio height/width 0.8–0.9; diameter of the first three whorls c. 0.85 mm, c. 1.75 mm, c. 3.7 mm respectively; number of whorls up to c. 3 3/4, height aperture up to 3.8 mm; width aperture up to 3.5 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2400-2700 m. In primary forest on

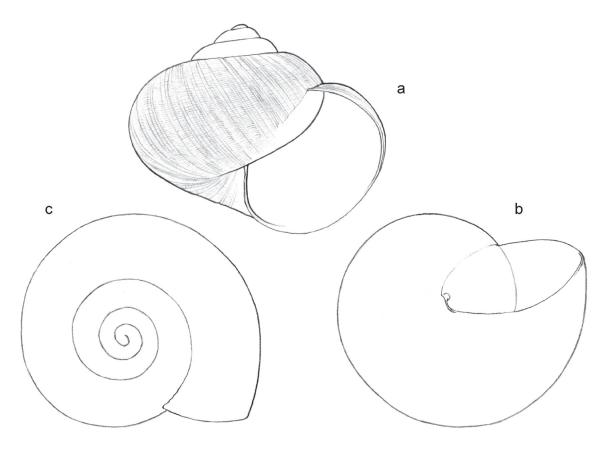


Fig. 91, a-c. 'Durgella' densestriata Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 5.5 mm high, b. Umbilical view, c. Apical view.

sandstone/shale or granodiorite bedrock. Endemic to Sabah.

Similar species elsewhere. Differs from *Durgella hosei* Godwin-Austen, 1891 (Sarawak), as well as continental Asiatic species listed in Blanford and Godwin-Austen (1908: 213), Godwin-Austen (1916: 555), and Solem (1966: 49), by the low-conical spire with slightly concave sides, as well as by the fine and dense spiral striation. *Note*. Generic position yet to be ascertained.

Genus *Hemiplecta* Albers, 1850

Diagnosis for the Sabah species. Shell calcareous, with or without spiral bands of distinctly different color. Shell above the periphery dull or with a silky luster, and with an uneven sculpture including small wrinkles and dents. Shell width in adults of 5–6 whorls 27.5–51.0 mm; ratio height/width 0.53–0.65. Umbilicus open, narrow, without spur protruding from the columellar corner.

Hemiplecta densa (A Adams & Reeve, 1850)

(fig. 92a-e, 96b, map 18d)

Godwin-Austen 1891: 26; Smith 1893a: 349; Schepman 1896: 150; Wiegmann 1898: 378; Von Martens 1908: 260; Haas 1951: 626; Solem 1964: 20; Saul 1967: 109; Maassen 2001: 102; Schilthuizen & Rutjes 2001: 421; Schilthuizen & Vermeulen 2003: 95; Schilthuizen et al. 2003b: 41, 42; Marzuki et al. 2021: 50. – *Helix densa* A Adams & Reeve 1850 (1848–1850): 62; Reeve 1852 (1851–1854): Pl. 73, fig. 375; Pfeiffer 1854 (1853–1860): 403. – *Nanina (Hemiplecta) densa* (A Adams & Reeve) Pfeiffer 1855b: 121; Bock 1881: 628; Pfeiffer & Clessin 1881: 52. – *Nanina densa* (A Adams & Reeve) Von Martens 1867: 230; Issel 1874: 395; Von Martens 1879 (1876–1879): 175; Aldrich 1889: 24. – Type from Philippines.

Helix nobilis Pfeiffer 1850 (1849): 127; Reeve 1852 (1851–1854): Pl. 74, fig. 381; Pfeiffer 1853 (1853–1860): 291. – Nanina (Ryssota) nobilis (L Pfeiffer) Pfeiffer 1855b: 121 ('Rhyssota'). – Nanina nobilis (L Pfeiffer) Issel 1874: 397; Tenison Woods 1888: 1021. – Hemiplecta nobilis (L Pfeiffer) Godwin-Austen 1891: 27. –

Type from 'Borneo'.

Helix schumacheriana Pfeiffer 1850a: 70; Metcalfe 1852 (1851): 70; Reeve 1852 (1851–1854): Pl. 73, fig. 379.

- Nanina (Hemiplecta) schumacheriana (L Pfeiffer) Pfeiffer 1855b: 121; Pfeiffer & Clessin 1881: 52.

- Hemiplecta schumacheriana (L Pfeiffer) Wallace 1865: 406; Von Martens 1908: 261; Schepman 1918: 159; Saul 1967: 109.

- Nanina schumacheriana (L Pfeiffer) Tenison Woods 1888: 1022; Dohrn 1889: 57.

- Type from 'Borneo'.

Helix donovani Pfeiffer 1851c: 26. – Nanina (Ryssota) donovani (L Pfeiffer) Pfeiffer 1855b: 121 ('Rhyssota'). – Nanina donovani (L Pfeiffer) Von Martens 1867: 233; Issel 1874: 396; Tenison Woods 1888: 1021. – Hemiplecta donovani (L Pfeiffer) Godwin-Austen 1891: 27. – Type of unknown origin.

Helix souleyetiana Pfeiffer 1853 (1851b): 252; Reeve 1852 (1851–1854): Pl. 73, fig. 378; Pfeiffer 1854 (1853–1860): 401. – Nanina (Ryssota) souleyetiana (L Pfeiffer) Pfeiffer 1855b: 121 ('Rhyssota'). – Nanina souleyetiana (L Pfeiffer) Von Martens 1867: 233; Issel 1874: 396; Tenison Woods 1888: 1021. – Type of unknown origin.

Nanina obliquata auct. Von Martens 1867: 235; Issel 1874: 33 (partly); Tenison Woods 1888: 1017 (partly). – Hemiplecta obliquata auct. Godwin-Austen 1891: 27; Von Martens 1908: 261.

Nanina (Hemiplecta) humphreysiana auct. Smith 1894b: 454. – Hemiplecta humphreysiana auct. Saul 1967: 109; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54; Phung et al. 2017: 71; Foon et al. 2018: 95.

[Not Helix humphreysiana Lea].

[Not Helix obliquata Reeve].

Description. Shell dextral, (very) large, rather thin to rather thick, opaque, olive-green to brown, with a narrow to wide, (dark) brown band just below the periphery, and often a narrow, pale or white band at the periphery. Surface shiny around the apex, otherwise dull or with a silky luster. Spire slightly raised to low-conical with (slightly) convex sides, apex narrowly rounded. Whorls: Apical whorls convex, other whorls above and below the periphery equally convex, namely slightly to moderately so; periphery rounded to acutely keeled. Suture not impressed, but outer whorl often slightly shouldered just below the suture. Sculpture. Protoconch approx. smooth, with a few slight radial riblets. Teleoconch. Radial sculpture: Growth lines, at uneven intervals raised or developing into slight, low riblets. Spiral sculpture: Above and just below the periphery with fine, wavy, locally braided, shallow, oblique grooves and dents; towards the basal side of the shell this sculpture is replaced by fine, dense, continuous spiral grooves. Aperture broadly and obliquely crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere slightly thickened, not spreading. Umbilicus open, narrow, deep. Dimensions. Height 18.0–28.3 mm; width 27.5–47.0 mm; ratio height/width 0.60–0.65; diameter of the first three whorls 2.0–2.8 mm, 4.5–6.0 mm, 9.0–12.0 respectively; umbilicus 2.7–4.5 mm diam.; number of whorls 5 3/8–6 1/4; height aperture 11.5–20.5 mm; width aperture 14.5–25.0 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1700 m. Dry or wet primary forest, dry coastal forest, secondary forest. On limestone, sandstone/shale and serpentinite bedrock, on alluvial soils. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: Malaysia (Peninsula), Indonesia (? Sumatra), Philippines; uncertain because of unsettled taxonomy, see below.

Variability. Highly variable in size, the height of the spire and the shape of the periphery.

Notes. 1. Extensive anatomical description in Wiegmann (1898).

- 2. *Hemiplecta densa* and *H. humphreysiana* (Lea, 1841) have similar shells and may turn out to be conspecific. Usually, the former has a more angular periphery to the last whorl and is somewhat more densely coiled. Borneo shells generally agree with *H. densa*, although shells with a rounded periphery occur.
- 3. Originally, *Helix obliquata* Reeve, 1852 was described as a Bornean species, a provenance doubted by the authors cited. Cilia & Abbas (2012) claim that the species is a Sumatran endemic, and we have not seen any Bornean material that can be attributed to this species. We exclude it from the Bornean fauna.

Hemiplecta montivagans Vermeulen & Liew, new species

(fig. 92f–i, map 18e)

Type specimens from Malaysia, Sabah, mount Trus Madi (holotype BOR/MOL 1034); ditto, Forestry chalet (paratype JV 13210/1 shell).

Hemiplecta egeria auct. Vermeulen 1996b: 285; Schilthuizen 2004: 94; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data.

[Not *Hemiplecta egeria* E A Smith].

Cross diagnosis. Differs from Hemiplecta densa by the shell shape of the last whorl: Immediately below the periphery, the shell surface is almost parallel to the coiling axis of the shell. Resembles Everettia klemmantanica

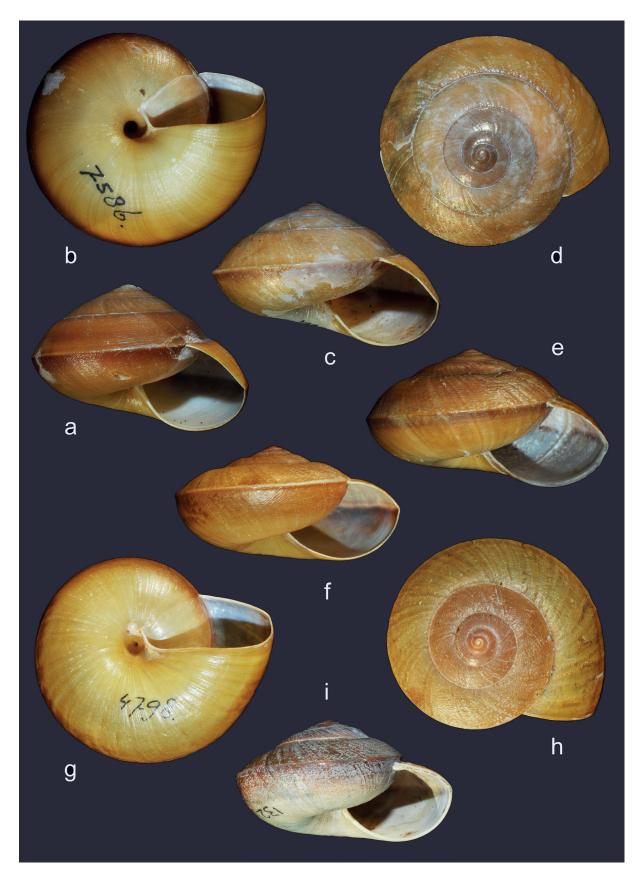


Fig. 92, a–e. *Hemiplecta densa* (A Adams & Reeve, 1850), a. Frontal view, shell 26 mm high, b. Umbilical view, c. Frontal view, shell 26 mm high; f–i. *Hemiplecta montivagans* Vermeulen & Liew, new species, f. Frontal view, shell 27 mm high, g. Umbilical view, h. Apical view, i. Frontal view, shell 28 mm high.

in general shape; differs by the oblique grooves and dents on the outer whorls, above the periphery.

Description. Shell dextral, very large, rather thin, opaque, brown(-green), with a wide, darker brown band just below the periphery. Surface dull or slightly silky above the periphery, somewhat shiny below. Spire slightly raised with approx. straight or slightly convex sides, apex narrowly rounded. Whorls slightly convex above the periphery, outer whorl slightly depressed just above the periphery; distinctly convex below the periphery with the shell surface almost parallel to the coiling axis just below the periphery; periphery distinctly but slightly obtusely keeled. Suture not impressed, but outer whorl with a slight depression just below the suture. Sculpture. Protoconch approx. smooth, with minute, dense radial riblets just below the suture. Teleoconch. Radial sculpture: Growth lines, at uneven intervals raised or developing into slight, low riblets; outer whorls just below the suture also with short wrinkles perpendicular to the suture. Spiral sculpture: Above and just below the periphery with rather fine, wavy, locally braided, shallow, oblique grooves and dents; towards the basal side of the shell this sculpture grades into a fine, still wavy but truly spiral grooves. Aperture broadly and obliquely crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere slightly thickened, not spreading. Umbilicus open, narrow, deep. Dimensions. Height 25–27 mm; width 46–51 mm; ratio height/width 0.53–0.54; diameter of the first three whorls 1.8–2.0 mm, 4.0–5.5 mm, 7.8–9.0 mm respectively; umbilicus 4.2–4.4 mm diam.; number of whorls 5 3/8–5 5/8; height aperture 16.6–17.0 mm; width aperture 24.0–26.5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 1000–1900 m. Dry or wet primary forest, secondary forest, also found in grassland in roadside. On sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Hemiplecta egeria E A Smith, 1895, from Palawan, is similar in shape but has a more depressed spire, a last whorl which is approx. flat above the periphery, and which turns obliquely inwards towards the coiling axis immediately below the periphery. It is also smaller: width c. 35 mm at 6 whorls.

Name derivation. From mons (Latin) = mountain, and vagare = to wander.

Genus Macrochlamys Gray, 1847

Diagnosis for the Sabah species. Shell calcareous, without spiral bands of distinctly different color. Shell above the periphery shiny or glossy, with or without an even sculpture, but without wrinkles and dents. Shell width in adults of 4–5 whorls 4.2–21 mm; ratio height/width 0.45–0.65. Umbilicus open, narrow, without spur protruding from the columellar corner.

Animal. Mantle lobes present, finger-shaped.

Anatomy. Penial structure: Vas deferens attached laterally to the epiphallus. Epiphallus with flagellum. Penis with a coiled caecum, retractor muscle attached distally to the caecum. Dart sac with a single, sessile apical gland. Dart absent. Gametolytic sac connected to the vagina by a long gametolytic duct.

Notes. 1. As a genus, Macrochlamys cannot be distinguished from Everettia (Dyakiidae) on shell characters alone. Most Sabah species have shells distinctly smaller than Sabah Everettia; only M. indica matches Sabah Everettia in size. See the cross diagnosis with M. indica, Everettia jucunda and E. jucundior. Living specimens of Macrochlamys are easily recognizable by the presence of one or more finger-shaped, mobile appendages on the mantle edge; these are absent in Everettia. Further differences can be found in the genitalia, compare the diagnosis of both genera and illustrations.

- 2. Macrochlamys has consistently larger shells than Microcystina.
- 3. Inclusion of *Macrochlamys subcorpulenta*, *M. tenuiarata*, and *M. trusmadiensis* is tentative and based on shell size.

Macrochlamys indica Godwin-Austen, 1883

(fig. 93a, 94a-c, 96c, map 18f)

Godwin-Austen 1883 (1882–1888): 97; Blanford et al. 1908: 95; Maassen 2001: 111; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Uchida et al. 2013: 53, 54; Phung et al. 2017: 74. – Type from India.

Cross diagnosis. Distinctly larger than other Sabah *Macrochlamys*, (shell height up to 12 mm, versus up to 5.5 mm; diameter third whorl 5.0–6.5 mm, versus 2.1–4.0 mm). It shares the smooth protoconch with *M. trilobata*; additional to the character above, the latter differs by the presence of radial sculpture on the upper surface of the shell.

Among Sabah Everettia, Macrochlamys indica resembles E. jucunda and E. jucundior. Everettia jucunda differs by the more slowly expanding outer whorls: Approx. 22 mm wide shells of E. jucunda have up to 6 3/4 whorls, a shell of similar size of M. indica only up to 5 1/2. The first 4 whorls of the two species develop in a comparable way; juveniles are therefore difficult to distinguish on shell characters. Everettia jucundior differs by the more distinct and continuous spiral sculpture on the last whorl, above the periphery.

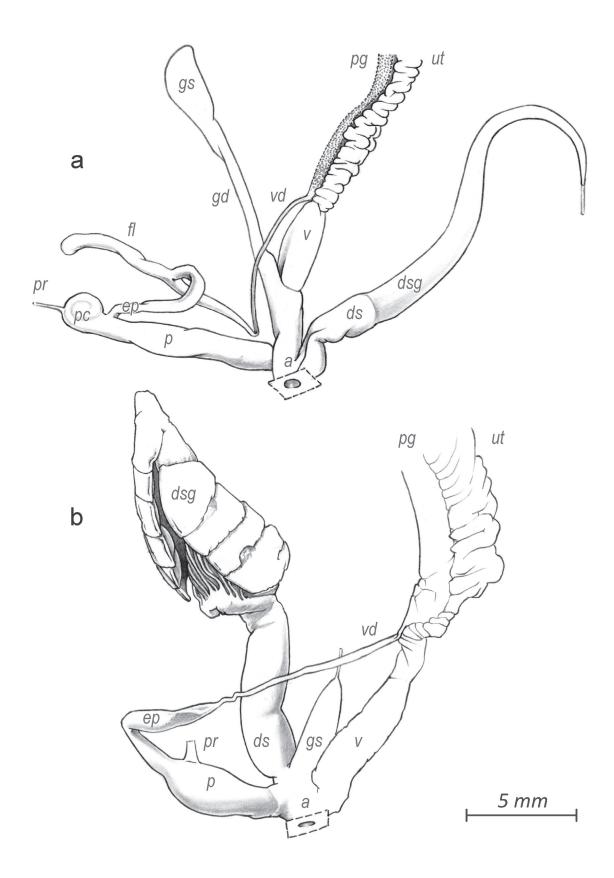


Fig. 93, a–b. Distal part of the genitals of *Macrochlamys* and *Everettia*, a. *Macrochlamys indica* Godwin-Austen, 1883; b, *Everettia corrugata corrugata* Laidlaw, 1937. Abbreviations: a = atrium; ds = dart sac; dsg = dart sac gland; ep = epiphallus; fl = flagellum; gd = gametolytic duct; gs = gametolytic sac; p = penis; pc = penis caecum; pg = prostate gland; pr = penis retractor muscle; ut = uterus; v = vagina; vd = vas deferens.

Description. Shell medium-sized to large, thin, slightly translucent to opaque, pale yellowish brown, often slightly paler in the umbilical area. Surface shiny, Outline lenticular, spire somewhat raised with a narrowly rounded apex. Whorls moderately convex; last whorl rounded at the periphery. Sculpture. Protoconch approx. smooth. Teleoconch with few somewhat unevenly scattered, inconspicuous, growth lines, which are often somewhat raised just below the suture. Spiral sculpture: Locally (particularly below the suture) very fine, inconspicuous, very densely placed grooves on the upper and lower surface. Aperture broadly crescent-shaped, peristome neither widened, nor thickened on the palatal and basal side. Umbilicus open, very narrow but deep; columellar side of the peristome rounded, not covering the umbilicus in adult shells. Dimensions. Height up to 12.0 mm; width up to 21.5 mm; ratio height/width 0.45-0.60; diameters of the first four whorls 1.3-1.9 mm, 3.0-3.6 mm, 5.0-6.5 mm, 9.0-11.0 mm respectively; number of whorls up to 5 1/2; height aperture up to 9.5 mm; width aperture up to 11.0 mm.

Distribution in Sabah. Scattered localities in W; elsewhere lower Kinabatangan only. Elevation range: 0-1100 m. In gardens. Introduced. Also in Sarawak. Distribution elsewhere: SE Asia. Natural range: India.

Macrochlamys infans (Reeve, 1854)

fig. 94d–f, 96d, map 19a)

Marzuki et al. 2021: 52. - Helix infans Reeve 1854 (1851-1854): Pl. 201, fig. 1417; Pfeiffer 1855 (1854b): 290. - Nanina infans (Reeve) Von Martens 1867: 243; Issel 1874: 401; Tenison Woods 1888: 1019. - Nanina (Macrochlamys) infans (Reeve) Pfeiffer & Clessin 1881: 44. – Microcystina infans (Reeve) Godwin-Austen 1891: 37; Von Martens 1908: 260. – Lamprocystis infans (Reeve) Van Benthem Jutting 1950: 412; 1959: 140. – Helicarion infans (Reeve) Schilthuizen et al. 2013: Online supplementary data. – Type from Borneo, Labuan. Nanina myops Dohrn & Semper 1862: 206. - Helix myops (Dohrn & J C Semper) Pfeiffer 1863 (1860-1866): 221. - Nanina (Microcystis) myops (Dohrn & J C Semper) Pfeiffer & Clessin 1881: 38. - Lamprocystis myops (Dohrn & J C Semper) Von Möllendorff 1894: 207; Smith 1895: 109. – Type from Philippines, Mindanao. Nanina tersa Issel 1874: 399; Tenison Woods 1888: 1012. - Microcystis tersa (Issel) Godwin-Austen 1891: 36; Von Martens 1908: 260. – Macrochlamys tersa (Issel) Schilthuizen et al. 2002: 256; Schilthuizen et al. 2003b:

41, 42; Schilthuizen 2004: 94; Clements et al. 2008: 2760, 2761; Liew et al. 2010: Online Supporting Information, Appendix S1: 2761; Schilthuizen et al. 2011: 4; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54; Phung et al. 2017: 74; Marzuki et al. 2021: 53. - Type from 'Borneo'.

Lamprocystis chlororaphe Smith 1893a: 348. – Type from Philippines, 'Palawan'.

Description. Shell very small, thin, slightly translucent to opaque, pale yellowish brown to dark red-brown, often slightly paler brown in the umbilical area. Surface silky above, slightly shinier below. Outline lenticular, spire somewhat raised to depressed-conical with an narrowly rounded apex. Whorls moderately convex; last whorl rounded at the periphery. Sculpture. Protoconch with minute, very slight, densely placed radial riblets and more than 20 thin, well-spaced, approx. continuous spiral grooves. Teleoconch. Radial sculpture: A few scattered, inconspicuous, locally somewhat raised growth lines. Spiral sculpture: Above the periphery very fine (as fine as on the protoconch, and just visible at 40x magnification), often continuous but sometimes inconspicuous, (very) densely placed grooves, below the suture and below the periphery often with slightly more distinct, more widely spaced grooves. Aperture (rather broadly) crescent-shaped, peristome neither widened, nor thickened on the palatal and basal side. Umbilicus closed or open, very narrow; columellar side of the peristome somewhat thickened, often angular and partly covering the umbilicus in adult shells. Dimensions. Height up to 3.7 mm; width up to 6.0 mm; ratio height/width 0.56-0.65; diameters of the first four whorls 0.8-1.1 mm, 1.5-1.9 mm, 2.5-3.3 mm, 4.4-5.6 mm respectively; number of whorls up to 4 5/8; height aperture up to 2.8 mm; width aperture up to 3.3 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0-1200 m. In wet or dry primary forest, coastal woodland, shrubby vegetation. Also in depleted primary vegetation to degraded secondary vegetation. On limestone, sandstone/shale or volcanic bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Indonesia (Sumatra, Java, Lesser Sunda islands), Philippines (Palawan).

Macrochlamys subcorpulenta Vermeulen & Liew, new species

(fig. 94g-i, map 19a)

Type from Malaysia, Sabah, upper Padas river valley, tributary of Matang river, S of Long Pasia (holotype BOR/ MOL 14839).

Cross diagnosis. Resembles Macrochlamys infans but differs by the spiral sculpture on the protoconch (c. 16 rows of minute pits, versus more than 20 approx. continuous spiral grooves), and by the virtual absence of spiral striation on the teleoconch, including the lower surface of the shell (versus very fine, sometimes inconspicuous, grooves on the upper surface, and often more widely spaced and more distinct grooves on the lower). From M. trusmadiensis, too, M. subcorpulenta differs by the absence of a fine but continuous spiral striation on the teleoconch.

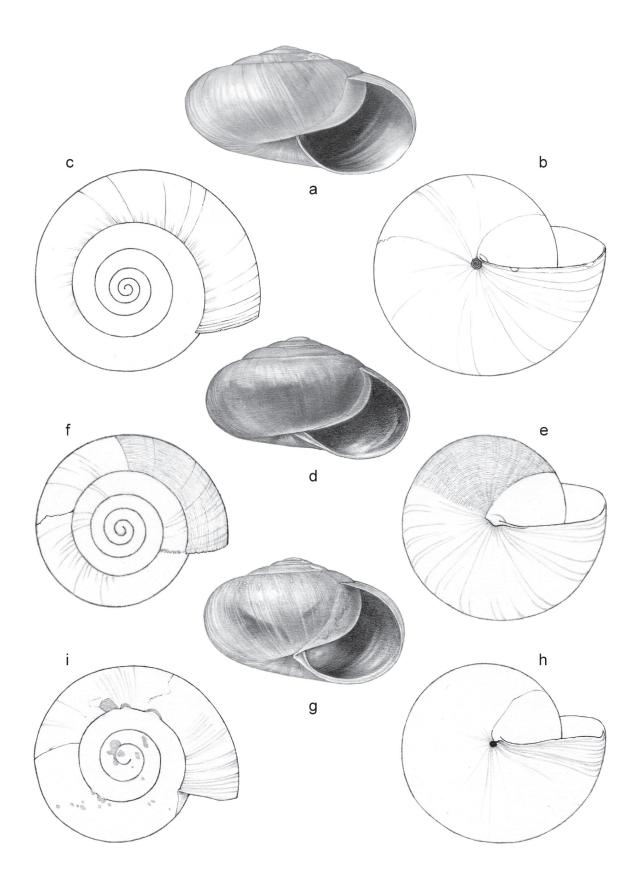


Fig. 94, a–c. *Macrochlamys indica* Godwin-Austen, 1883, a. Frontal view, shell 10.8 mm high, b. Umbilical view, c. Apical view; d–f. *Macrochlamys infans* (Reeve, 1854), d. Frontal view, shell 3.6 mm high, e. Umbilical view, f. Apical view; g–i. *Macrochlamys subcorpulenta* Vermeulen & Liew, new species, g. Frontal view, shell 2.4 mm high, h. Umbilical view, i. Apical view.

Description. Shell very small, thin, slightly translucent, yellowish corneous. Surface glossy. Outline lenticular, spire somewhat raised, apex rounded. Whorls moderately convex; last whorl rather broadly rounded at the periphery. Sculpture. Protoconch with minute, very slight, densely placed radial riblets and c. 16 thin, well-spaced spiral rows of minute pits in between the riblets. Teleoconch. Radial sculpture: A few inconspicuous growth lines only. Spiral sculpture virtually absent, locally some traces of fine striation (finer than on the protoconch, and just visible at 40x magnification), particularly below the suture. Aperture (broadly) crescent-shaped, peristome neither widened, nor thickened on the palatal and basal side. Umbilicus open but very narrow; columellar side of the peristome somewhat thickened, angular but not covering the umbilicus. Dimensions. Height c. 2.5 mm; width c. 3.9 mm; ratio height/width c. 0.64; diameters of the first three whorls c. 0.8 mm, c. 1.6 mm, c. 2.9 mm respectively; number of whorls c. 3 1/2; height aperture c. 1.9 mm; width aperture c. 2.0 mm.

Distribution in Sabah. Highlands: Upper Padas only. Elevation: c. 1100 m. In damp primary forest on sand-stone/shale vegetation. Endemic to Sabah.

Note. The single specimen available is probably subadult.

Name derivation. From corpulentus (Latin) = fat, with the prefix sub- = a little.

Macrochlamys tenuiarata Vermeulen & Liew, new species

(fig. 95a-d, map 18e)

Type from Malaysia, Sabah, Crocker Range N.P., Gua Laing (holotype BOR/MOL 15010, paratypes JV 1127/14 shells).

Cross diagnosis. Among Sabah Macrochlamys identified by the widely and unevenly spaced, very shallow, vaguely outlined radial furrows above the periphery. The spiral sculpture is also diagnostic: On the protoconch 7–12 approx. continuous (not divided into rows of tiny pits, as in M. subcorpulenta), widely spaced grooves, on the teleoconch at most traces of a very fine and dense striation locally, much finer and denser than on the protoconch (not approx. similar to the spiral sculpture on the protoconch, as in M. infans and M. trusmadiensis). Macrochlamys trilobata has a similar, but more densely placed radial sculpture, and the whorls expand more rapidly (fourth whorl 5.8–7.0 mm wide, versus 3.4–3.7 mm).

Description. Shell very small, thin, opaque, pale brown, often almost white, slightly paler brown in the umbilical area. Surface shiny. Outline lenticular, spire somewhat raised to depressed-conical with convex sides and a rounded apex. Whorls moderately convex; last whorl rounded at the periphery. Sculpture. Protoconch approx. without radial sculpture, with 7–12 thin, widely spaced, approx. continuous spiral grooves. Teleoconch. Radial sculpture: Few inconspicuous growth lines, next to these with widely and unevenly spaced, very shallow, vaguely outlined radial depressions above the periphery, which gradually disappear below the periphery. Spiral sculpture virtually absent or inconspicuous: Above the periphery locally traces of very fine and dense striation (much finer and denser than on the protoconch), often slightly more distinct just below the suture, below the periphery as fine and dense as above the periphery but often somewhat more continuous. Aperture (broadly) crescent-shaped, peristome neither widened, nor thickened on the palatal and basal side. Umbilicus closed or open, very narrow; columellar side of the peristome somewhat thickened and often angular and partly or entirely covering the umbilicus in adult shells. Dimensions. Height up to 3.0 mm; width up to 5.3 mm; ratio height/width 0.56–0.65; diameters of the first four whorls 0.65–0.70 mm, 1.20–1.35 mm, 2.1–2.4 mm, 3.4–3.7 mm respectively; number of whorls up to 4 3/4; height aperture up to 2.1 mm; width aperture up to 2.8 mm.

Distribution in Sabah. Crocker range only. Elevation range: 600–700 m. In depleted primary forest on limestone bedrock. Endemic to Sabah.

Name derivation. From tenuis (Latin) = fine, and arare = to plough, referring to the fine sculpture.

Macrochlamys trilobata Vermeulen & Liew, new species

(fig. 95e–g, 96e, map 18f)

Type from Malaysia, Sabah, mount Tambuyukon summit (holotype BOR/MOL 14714).

Cross diagnosis. Among Sabah Macrochlamys characterized by the rather fine, rather evenly spaced and rather densely placed, shallow radial undulations above the periphery. In M. tenuiarata a similar sculpture occurs, but the undulations are much more widely spaced; next to this, the whorls in M. trilobata expand more rapidly (fourth whorl 5.8–7.0 mm wide, versus 3.4–3.7 mm). In size and coiling mode M. trilobata resembles M. infans, but next to the presence of radial sculpture it differs by the absence of spiral striation, and by the somewhat wider aperture.

Description. Shell small, thin, slightly translucent, yellowish brown to red-brown. Surface shiny. Outline lenticular, spire somewhat raised with a rounded apex. Whorls moderately convex; last whorl rounded at the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: A few scattered, inconspicuous, locally somewhat raised growth lines, and with rather fine, rather evenly spaced and rather densely placed, very shallow, vaguely outlined radial depressions, creating an undulating surface, most conspicuously so above the periphery.

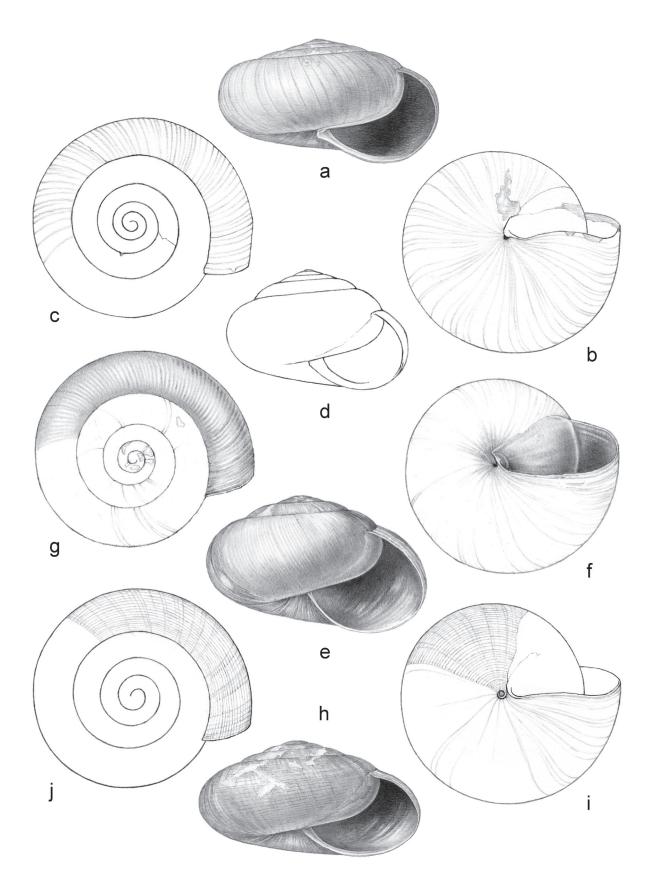


Fig. 95, a–d. *Macrochlamys tenuiarata* Vermeulen & Liew, new species, a. Frontal view, shell 3.0 mm high, b. Umbilical view, c. Apical view, d. Frontal view, shell 2.8 mm high; e–g. *Macrochlamys trilobata* Vermeulen & Liew, new species, e. Frontal view, shell 5.4 mm high, f. Umbilical view, g. Apical view; h–j. *Macrochlamys trusmadiensis* Vermeulen & Liew, new name, h. Frontal view, shell 2.3 mm high, i. Umbilical view, j. Apical view.

Spiral sculpture absent. Aperture broadly crescent-shaped, peristome neither widened, nor thickened on the palatal and basal side. Umbilicus open, very narrow; columellar side of the peristome not thickened, often angular and partly covering the umbilicus in adult shells. Dimensions. Height up to 5.5 mm; width up to 8.7 mm; ratio height/width 0.62–0.65; diameters of the first four whorls c. 1.0 mm, 1.8–2.0 mm, 3.3–4.0 mm, 5.8–7.0 mm respectively; number of whorls up to 4.7/8; height aperture up to 4.0 mm; width aperture up to 4.5 mm.

Animal. Mantle edge with 3 lobes, the longest attached at the shell periphery.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu. Elevation range: 2500–3400 m. Primary and secondary forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Name derivation. From trilobatus (Latin) = with three lobes.

Macrochlamys trusmadiensis Vermeulen & Liew, new name

(fig. 95h-j, map 18f)

Microcystina planiuscula Vermeulen et al. 2015: 50. – Type from Malaysia, Sabah, mount Trus Madi, Gua Dawaras. [Not *Helix planiuscula* Hutton. – *Macrochlamys* (?) *planiuscula* (Hutton) Godwin-Austen, 1908].

Cross diagnosis. Resembles *Macrochlamys infans* and *M. subcorpulenta*, differs by the distinct, widely spaced spiral sculpture: On the protoconch 7–12 grooves (versus more than 16 grooves); on the teleoconch widely and sometimes unevenly spaced continuous, grooves on the upper surface (versus at most very fine, often continuous but sometimes inconspicuous, densely placed grooves). Also, the whorls are slightly narrower (third whorl 2.3–2.5 mm wide, versus 2.5–3.3 mm).

Description. Shell very small, thin, translucent to opaque, yellowish brown. Surface glossy above, silky below. Outline lenticular, spire somewhat raised. Whorls moderately convex; last whorl rounded at the periphery. Sculpture. Protoconch without radial riblets; with 7–12 very fine, continuous, widely and evenly spaced spiral grooves. Teleoconch. Radial sculpture: Few scattered, inconspicuous growth lines. Spiral sculpture: Fine, widely (approx. as on the protoconch) and sometimes unevenly spaced, continuous grooves on the upper surface; similar but somewhat more distinct grooves on the lower surface. Aperture broadly crescent-shaped, peristome neither thickened, nor spreading on the palatal and basal side. Umbilicus open, narrow; columellar side of the peristome somewhat thickened, rounded. Dimensions. Height up to 2.3 mm; width up to 4.2 mm; ratio height/width 0.55–0.59; diameters of the first four whorls 0.7–0.8 mm, 1.2–1.4 mm, 2.3–2.5 mm, c. 4.1 mm respectively; number of whorls up to 4 1/8; height aperture up to 1.5 mm; width aperture up to 2.1 mm.

Distribution in Sabah. Highlands: Trus Madi range only. Elevation range: 1000–1500 m. In primary forest on limestone bedrock. Endemic to Sabah.

Name derivation. The name refers to the Trus Madi range, where the species occurs.

Genus Microcystina Mörch, 1872

Diagnosis for the Sabah species. Shell calcareous, without spiral bands of distinctly different color. Shell above the periphery shiny or glossy, with or without a fine and even sculpture, but without wrinkles and dents. Shell width in adults of 4–5 whorls 1.9–3.6 mm; ratio height/width 0.53–0.66(–0.80). Umbilicus closed or open, narrow, often partly or entirely covered by a minute, triangular spur protruding from the columellar corner of the peristome; this spur lacking or inconspicuous in juveniles.

Notes. 1. All sculpture is very fine and inconspicuous, and as a result the shell surface seems smooth at first impression. This distinguishes the smaller species of *Microcystina* (particularly *M. sinica*) from sympatric *Sundacharopa* species (Charopidae), which have similar shells with a more conspicuous sculpture.

- 2. Bornean *Macrochlamys* and *Everettia* (Ariophantidae), and *Helicarion* (Helicarionidae) have similarly shaped shells, including the inconspicuous sculpture, but they are larger (width of adult shells 4.2 mm or more).
 - 3. Placement of *Microcystina* into the family Ariophantidae follows Schileyko (2003).

KEY TO THE GROUPS

1 - Shell whiteGroup 11 - Shell pale corneous, to yellowish green or brownGroup 2

Group 1

Microcystina callifera Vermeulen, Liew & Schilthuizen, 2015

(fig. 97a-c, 100a, map 19b)

Vermeulen et al. 2015: 44; Phung et al. 2017: 76. – Type from Malaysia, Sabah, Mantanani islands, Lungisan *island*.

Microcystina callifera, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplemen-



Fig. 96, a. 'Durgella' densestriata Vermeulen, Liew & Schilthuizen, 2015; b. Hemiplecta densa (A Adams & Reeve, 1850); c. Macrochlamys indica Godwin-Austen, 1883; d. Macrochlamys infans (Reeve, 1854); e. Macrochlamys trilobata Vermeulen & Liew, new species; f. Vitrinula baramensis (Kobelt, 1897), juvenile; g. Vitrinula decrespignyi (Higgins, 1868); h. Vitrinula padasensis (E A Smith, 1895).

tary data.

Cross diagnosis. Uniquely identified within *Microcystina* by the callus on the columellar side of the aperture. The spiral sculpture is usually more distinct, and more widely spaced than in *M. striatula*.

Description. Shell very small, (rather) thin, almost opaque or slightly translucent, white. Surface with a silky luster. Outline lenticular; spire almost flat to moderately elevated. Whorls slightly convex. Sculpture. Protoconch with fine, widely spaced, shallow radial riblets towards the teleoconch; with inconspicuous, widely spaced, continuous, shallow, vaguely outlined spiral grooves. Teleoconch. Radial sculpture: Inconspicuous growth lines, in some specimens locally grading into unevenly and rather densely placed to widely spaced, shallow grooves. Spiral sculpture: Upper surface with very fine, widely spaced, continuous, moderately raised, sharply outlined spiral threads; lower surface with equally fine, widely spaced, shallow grooves. This spiral sculpture is sometimes rather distinct, sometimes inconspicuous and patchy. Aperture crescent-shaped, peristome with a distinct callus on the columellar side, not spreading. Umbilicus closed by a callous extension of the columellar corner of the peristome, the same callus also narrowing the aperture on the columellar side. Dimensions. Height up to 1.5 mm; width up to 2.5 mm; diameters of the first three whorls 0.5–0.6 mm, 0.9–1.0 mm, 1.2–1.4 mm respectively; number of whorls up to 4 1/2; height aperture up to 1.0 mm; width aperture up to 1.4 mm.

Distribution in Sabah. Islands in W and N: Mantanani islands, Banggi island. Elevation range: 0–100 m. In coastal woodland on limestone bedrock. Elevation range: 0–100 m. Endemic to Sabah.

Note. The callus on the columellar side of the aperture is present in all adult specimens, and therefore not likely to be a malformation.

Microcystina microrhynchus Vermeulen, Liew & Schilthuizen, 2015 (fig. 97d–f, map 19c)

Vermeulen et al. 2015: 40; Phung et al. 2017: 75; Foon et al. 2018: 95. – Type from Malaysia, Sabah, Interior Prov., Gua Pungiton.

Microcystina sp. 'BO-01' Schilthuizen et al. 2002: 256, 257; Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 94.

Microcystina microrhynchus, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

Microcystina sp. Schilthuizen et al. 2011: 5.

Cross diagnosis. Characterized among Bornean *Microcystina* with white shells by a complete absence of spiral striation. Usually, it is also larger and has more rapidly expanding whorls (diameter of the third whorl 1.5–2.5 mm, versus 1.2–1.5 mm).

Description. Shell very small, thin, translucent, white. Surface glossy. Outline lenticular; spire almost flat or slightly elevated. Whorls slightly convex. Sculpture. Protoconch: Smooth, sometimes with a few inconspicuous, scattered radial riblets only. Teleoconch. Radial sculpture: Inconspicuous growth lines and widely but unevenly spaced, shallow grooves, often alternating with areas of a much finer, denser but equally unevenly spaced striation; sometimes the latter striation is predominant. Spiral sculpture absent. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus partly or entirely covered by a minute, triangular spur protruding from the columellar corner of the peristome; this spur lacking or inconspicuous in juveniles; umbilical region moderately concave. Dimensions. Height up to 1.7 mm; width up to 3 mm; diameters of the first three whorls 0.5–0.8 mm, 0.9–1.5 mm, 1.5–2.5 mm respectively; number of whorls up to 4 1/8; height aperture up to 1.4 mm; width aperture up to 1.7 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–3500 m. In rainforest, periodically dry, shrubby woodland, coastal woodland, secondary forest and other degraded vegetation; on limestone, sandstone/shale and granitic bedrock. Also in Brunei, Sarawak, Kalimantan. Endemic to Borneo.

Similar species elsewhere. Resembles Lamprocystis vitreiformis Von Möllendorff, 1897 (Indonesia: Sumatra, Java, and Bali); see Vermeulen and Whitten (1998: 118); Microcystina microrhynchus differs by the minute spur protruding from the columellar corner of the peristome and covering the umbilicus. Microcystina chionodiscus Vermeulen, 1996 (Indonesia, Bali); see Vermeulen and Whitten (1998: 115), has a smaller first whorl than M. microrhynchus (diameter 0.4–0.5 mm, versus 0.5–0.8 mm).

Microcystina striatula Vermeulen, Liew & Schilthuizen, 2015 (fig. 97g–i, 100b, map 19d)

Vermeulen et al. 2015: 44; Phung et al. 2017: 74. - Type from Malaysia, Sabah, Tabin valley.

Microcystina striatula, unavailable name, Clements et al. 2008: 2761.

Microcystina sp. 'BO-02' Schilthuizen & Vermeulen 2003a: 95; Schilthuizen et al. 2003b: 41.

Cross diagnosis. Differs at first sight from Microcystina microrhynchus by the presence of a fine spiral stri-

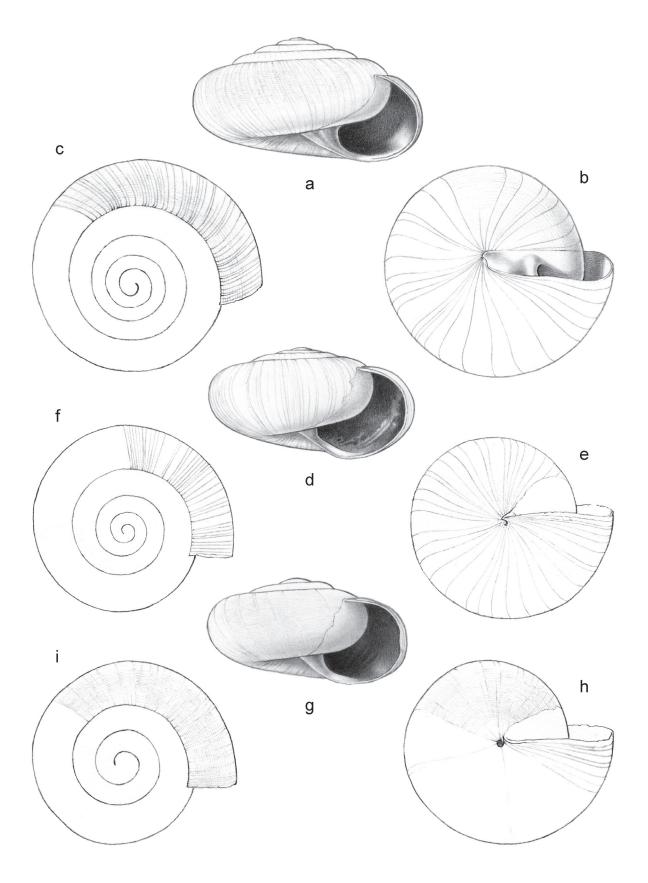


Fig. 97, a–c. *Microcystina callifera* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.4 mm high, b. Umbilical view, c. Apical view; d–f. *Microcystina microrhynchus* Vermeulen, Liew & Schilthuizen, 2015, d. Frontal view, shell 1.6 mm high, e. Umbilical view, f. Apical view; g–i. *Microcystina striatula* Vermeulen, Liew & Schilthuizen, 2015, g. Frontal view, shell 0.8 mm high, h. Umbilical view, i. Apical view.

ation, giving the shell surface a soft, silky shine rather than a high gloss. Next to that, the umbilical area is more distinctly concave.

Description. Shell very small, thin, (slightly) translucent, white. Surface with a silky luster. Outline lenticular, spire almost flat to slightly elevated. Whorls slightly to moderately convex. Sculpture. Protoconch sometimes with fine, moderately spaced, shallow radial grooves towards the teleoconch; with a very fine (hardly visible at 40x magnification), densely placed, continuous, shallow, vaguely outlined spiral striation. Teleoconch. Radial sculpture: Inconspicuous growth lines, sometimes a few scattered, slight grooves. Spiral sculpture: Very fine (just visible at 40x magnification) only slightly spaced, continuous, shallow, rather vaguely outlined grooves on the upper surface; and similar, but more densely placed grooves on the lower surface. This spiral sculpture is inconspicuous and patchy in some shells. Aperture rather broadly crescent-shaped, peristome not thickened, not spreading. Umbilicus open, narrow, inner wall with an obtuse peripheral edge; umbilical region distinctly concave. Dimensions. Height up to 1.1 mm; width up to 1.9 mm; diameters of the first three whorls 0.4–0.5 mm, 0.8–0.9 mm, 1.4–1.5 mm respectively; number of whorls up to 3 3/4; height aperture up to 0.8 mm; width aperture up to 1.0 mm.

Distribution in Sabah. Widespread, less common than Microcystina microrhynchus. Elevation range: 0–1200 m. In rainforest, seasonally dry coastal forest and shrubby forest, on limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Similar species elsewhere. Resembles Microcystina chionodiscus Vermeulen, 1996 (Indonesia, Bali), but M. striatula has a more distinct spiral striation.

Note. SEM images at 400x magnification show that the areas in between the spiral grooves on the upper surface of the teleoconch have a 'welded' appearance which is unique among Sabah *Microcystina*.

Group 2

Microcystina appendiculata (Von Möllendorff, 1893)

(fig. 98a-c, map 19b)

Vermeulen et al. 2015: 50. – *Lamprocystis appendiculata* Von Möllendorff 1893: 72. – Type from Philippines, Leyte.

Microcystina lissa, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

Microcystina sp. 'BO-03' Schilthuizen et al. 2002: 256, 257; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42.

Cross diagnosis. The only Sabah species of *Microcystina*, Group 2 with a peristome extension covering the umbilicus. Resembles *M. planiuscula*, but has less rapidly expanding whorls, and has a finer spiral striation. Juveniles with an inconspicuous spur on the columellar side of the peristome can be distinguished from *M. physotrochus* by the lack of radial riblets on the protoconch and by with the flat, not convex, sides of the spire.

Description. Shell very small, thin, somewhat translucent, brown. Surface glossy. Outline lenticular; spire slightly to moderately elevated, depressed conical with a rounded apex. Whorls slightly convex. Sculpture. Protoconch without radial riblets; with 6–10 very fine, well-spaced, continuous, shallow spiral grooves. Teleoconch. Radial sculpture: Inconspicuous growth lines and a few unevenly spaced, very slight grooves. Spiral sculpture: Very fine, moderately to widely spaced, continuous, shallow, rather vaguely outlined spiral grooves on the top whorls, in adults usually absent on the last whorl above the periphery, but more frequently present, more densely placed, below the periphery. Spiral sculpture rarely entirely absent. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus partly or entirely covered by a minute, semi-elliptic to triangular spur protruding from the columellar corner of the peristome, this spur often less conspicuous in juveniles. Dimensions. Height up to 1.9 mm; width up to 3.3 mm; diameters of the first three whorls 0.5–0.6 mm, 0.9–1.2 mm, 1.5–1.9 mm respectively; number of whorls up to 4 3/4; height aperture up to 1.3 mm; width aperture up to 1.9 mm.

Distribution in Sabah. Rather common in E, common locally (lower Kinabatangan); elsewhere rare: Crocker range, Sapulut. Elevation range: 0–500(–1400) m. In primary and secondary forest on limestone and sandstone/shale bedrock. Distribution elsewhere: Philippines (Palawan, Leyte).

Similar species elsewhere. Microcystina cavernae Godwin-Austen, 1891 (Sarawak), has a shell of similar shape and color; it differs in lacking the columellar spur.

Microcystina consobrina Van Benthem Jutting, 1959

(fig. 98d–g, 100d, map 19b)

Van Benthem Jutting 1959: 145; Vermeulen & Whitten 1998: 115, 155; Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 49. – Type from Indonesia, Sumatra, Brastagi.

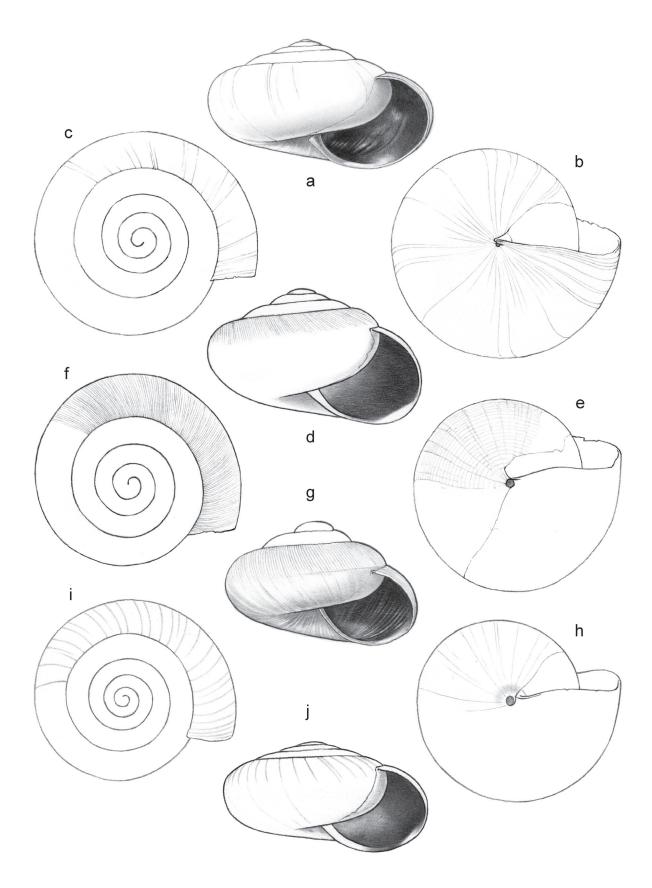


Fig. 98, a–c. *Microcystina appendiculata* (Von Möllendorff, 1893), a. Frontal view, shell 1.7 mm high, b. Umbilical view, c. Apical view; d–g. *Microcystina consobrina* Van Benthem Jutting, 1959, d. Frontal view, shell 1.4 mm high, e. Umbilical view, f. Apical view, g. Frontal view, shell 1.2 mm high; h–j. *Microcystina gratilla* Van Benthem Jutting, 1950, h. Frontal view, shell 2.0 mm high, i. Umbilical view, j. Apical view.

Cross diagnosis. Uniquely characterized within Group 2 by the fine and dense radial ribbing above the periphery.

Description. Shell very small, thin, translucent, pale yellowish green to yellowish brown. Surface shiny, glossy below. Outline approx. lenticular, spire moderately elevated, conical with a rounded apex. Whorls moderately to distinctly convex. Sculpture. Protoconch with fine, densely placed, low radial riblets towards the teleoconch, which are slightly coarser than those on the teleoconch; without spiral sculpture. Teleoconch. Radial sculpture: Above the periphery very fine, densely and evenly placed, low riblets; below the periphery with some unevenly spaced growth lines only. Spiral sculpture above the periphery absent or inconspicuous, below the periphery numerous fine, well-spaced, continuous, shallow, rather vaguely outlined grooves. Aperture rather broadly crescent-shaped, peristome not thickened, not spreading. Umbilicus open, narrow; columellar side of the peristome somewhat thickened but not covering the umbilicus. Dimensions. Height up to 1.4 mm; width up to 2.3 mm; diameters of the first three whorls 0.5–0.6 mm, 0.8–1.0 mm, 1.4–1.6 mm respectively; number of whorls up to 4 1/4; height aperture up to 1.0 mm; width aperture up to 1.2 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range. Elevation range: 2100–3500 m, elsewhere at 0–1700 m. In primary forest, on sandstone/shale and granodiorite bedrock. Distribution elsewhere: Indonesia (Sumatra, Bali).

Variability. The Kinabalu material has slightly coarser radial riblets than the type. The description includes material from elsewhere.

Similar species elsewhere. Resembles Lamprocystis exigua Von Möllendorff, 1897 (Indonesia: Java to Flores); see Van Benthem Jutting (1950: 447), which differs by having a larger first whorl (diameter 0.7–0.8 mm).

Microcystina gratilla Van Benthem Jutting, 1950

(fig. 98h–j, 100g–h, map 19e)

Van Benthem Jutting 1950: 448; 1959: 144; Saul 1967: 110; Vermeulen & Whitten 1998: 117, 155; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 44. — *Wilhelminaia gratilla* (Van Benthem Jutting) Maassen 2001: 96. — Type from Indonesia, Java, near Bogor.

Microcystina sp. 'BO-04', Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 94.

Cross diagnosis. Resembles Microcystina muscorum, but the sculpture, at least on the protoconch, is different; see below M. muscorum. Juvenile M. appendiculata in which the spur protruding from the columellar corner of the peristome has not yet developed can be distinguished by the absence of well-spaced radial grooves on the teleoconch. Juvenile M. physotrochus has a protoconch with more distinct radial riblets.

Description. Shell very small, thin, translucent, (yellowish) brown. Surface glossy. Outline lenticular; spire almost flat to moderately elevated, conical with a rounded apex. Whorls moderately convex. Sculpture. Protoconch with or without a few inconspicuous, scattered radial riblets towards the teleoconch; spiral striation absent. Teleoconch. Radial sculpture: Inconspicuous growth lines, next to these inconspicuous to distinct, well-spaced to densely placed, shallow grooves, often at uneven intervals. Spiral sculpture: Often traces of very fine (only just visible at 40x magnification), widely and somewhat unevenly spaced, shallow, rather sharply outlined grooves which are somewhat interrupted towards the protoconch, but which are continuous on the outer whorls. Aperture rather broadly crescent-shaped, peristome not thickened, not spreading. Umbilicus open, narrow, columellar side of the peristome somewhat thickened but not covering the umbilicus. Dimensions. Height up to 2.2 mm; width up to 3.6 mm; diameters of the first three whorls 0.4–0.5 mm, 0.8–1.0 mm, 1.2–1.6 mm respectively; number of whorls up to 4 7/8; height aperture up to 1.3 mm; width aperture up to 1.3 mm.

Distribution in Sabah. Highlands and adjacent hills in W: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 500–1300 m, elsewhere at 0–2400 m. In primary and secondary forest on sandstone/shale bedrock. Also in Kalimantan. Distribution elsewhere: Indonesia (Java, Madura, Bali, Flores). Variability. Most Sabah shells have a comparatively high spire.

Microcystina muscorum Van Benthem Jutting, 1959

(fig. 99a-c, 100e-f, map 19f)

Van Benthem Jutting 1959: 146; Vermeulen & Whitten 1998: 117, 155; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 53; Phung et al. 2017: 76. — Wilhelminaia muscorum (Van Benthem Jutting) Maassen 2001: 97. — Type from Indonesia, Sumatra, Berastagi.

Microcystina sp. 'BO-05', Schilthuizen et al. 2003a: 96; Schilthuizen 2004: 94.

Cross diagnosis. Usually well-characterized by the spiral striation consisting of minute, elongated pits. Rare populations (one in Sabah) lack this striation on the teleoconch. On the protoconch, however, the pits are always

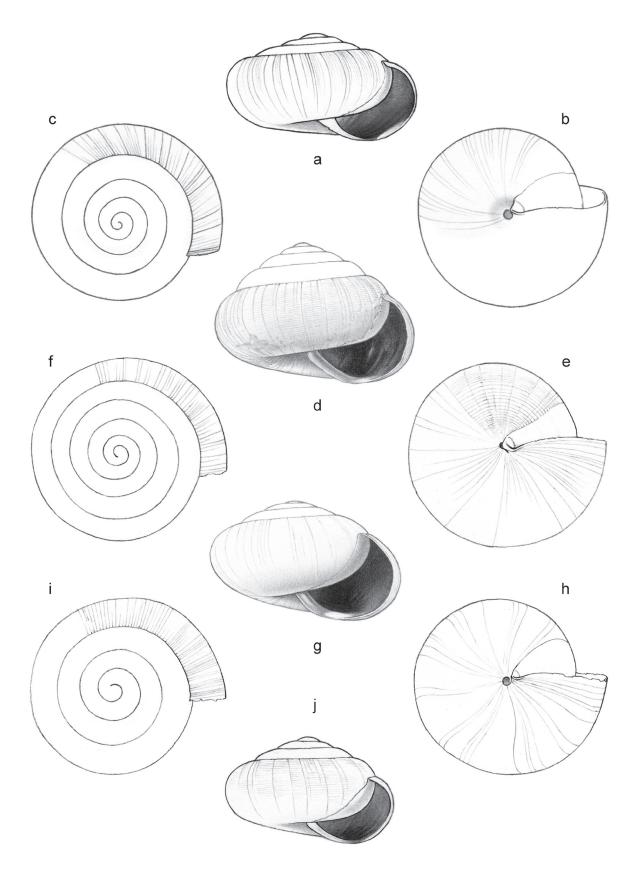


Fig. 99, a–c. *Microcystina muscorum* Van Benthem Jutting, 1959, a. Frontal view, shell 1.2 mm high, b. Umbilical view, c. Apical view; d–f. *Microcystina physotrochus* Vermeulen, Liew & Schilthuizen, 2015, d. Frontal view, shell 2.0 mm high, e. Umbilical view, f. Apical view; g–j. *Microcystina sinica* Von Möllendorff, 1885, g. Frontal view, shell 1.0 mm high, h. Umbilical view, i. Apical view, j. Frontal view, shell 0.6 mm high.

present, which serves to distinguish *Microcystina muscorum* from *M. gratilla. Microcystina sinica* has a similarly pitted protoconch, see under that species.

Description. Shell very small, thin, translucent, straw yellow to brown. Surface shiny. Outline approx. lenticular, spire moderately elevated, conical with a rounded apex. Whorls moderately convex. Sculpture. Protoconch with or without patches of fine, densely placed riblets; with a fine, moderately spaced spiral striation consisting of rows of minute, rather sharply outlined pits which are arranged in a reticulate pattern towards the teleoconch. Teleoconch. Radial sculpture: Inconspicuous growth lines, next to these with inconspicuous to distinct, well-spaced to densely placed, very shallow grooves, often at uneven intervals. Spiral sculpture: Above the periphery a very fine (just visible at 40x magnification), dense and evenly spaced spiral striation, the striae consisting of rows of disconnected or partially connected, minute, rather deep, sharply outlined pits (best visible in tangential light); below the periphery the pits are sometimes approx. connected to continuous grooves. Spiral sculpture sometimes absent on the teleoconch. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus open, narrow, columellar side of the peristome somewhat thickened but not covering the umbilicus. Dimensions. Height up to 1.9 mm; width up to 3.1 mm; diameters of the first three whorls 0.3–0.5 mm, 0.6–0.9 mm, 1.1–1.5 mm respectively; number of whorls up to 5 1/4; height aperture up to 1.2 mm; width aperture up to 1.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2500 m. In primary and secondary forest, coastal woodland, on limestone and sandstone/shale bedrock. Distribution elsewhere: Laos, Malaysia (Peninsula), Indonesia (Sumatra, Java, Bali).

Microcystina physotrochus Vermeulen, Liew & Schilthuizen, 2015

(fig. 99d–f, map 20a)

Vermeulen et al. 2015: 57; Phung et al. 2017: 71; Marzuki et al. 2021: 66. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Batu Keruak 2, near Sukau.

Microcystina physotrochus, unavailable name, Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data.

Cross diagnosis. Generally identified among Sabah *Microcystina* by the somewhat inflated shell. Relatively flat specimens differ from *M. appendiculata* by the absence of the spur on the columellar side of the peristome. *Philalanka anomphala* (Endodontidae) has a thinner shell, with much coarser, raised growth lines.

Description. Shell very small, thin, slightly translucent, brown. Surface glossy. Outline inflated-lenticular to depressed-ovoid; spire (moderately) elevated (more distinctly elevated in some adults) conical with convex sides or depressed-ovoid, with a rounded apex. Whorls moderately convex. Sculpture. Protoconch with patches of fine, densely placed radial riblets, particularly below the suture, and with or without very fine (only just visible at 40x magnification), well-spaced, somewhat interrupted, shallow, rather sharply outlined spiral grooves. Teleoconch. Radial sculpture: Inconspicuous growth lines, next to these rather distinct, well-spaced to densely placed shallow grooves, often at uneven intervals. Spiral sculpture: Fine, well-spaced, shallow spiral grooves on the upper and lower surface; sometimes only present on part of the shell, or (almost) entirely absent. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus open, narrow; columellar side of the peristome somewhat thickened but not covering the umbilicus. Dimensions. Height up to 2.3 mm; width up to 2.9 mm; diameters of the first three whorls 0.5–0.7 mm, 0.9–1.2 mm, 1.3–1.8 mm respectively; number of whorls up to 4 7/8; height aperture up to 1.5 mm; width aperture up to 1.6 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2700 m. In rainforest, seasonally dry forest, coastal forest, secondary woodland; on limestone and sandstone/shale bedrock. Usually found in small numbers. Also in Sarawak. Endemic to Borneo.

Similar species elsewhere. Species with a similar inflated-lenticular or depressed-ovoid shell of comparable size are: Sitala infantilis E A Smith, 1895 (Philippines, Palawan), with a corneous shell with a larger aperture, and a smooth surface; Microcystina seclusa Godwin-Austen, 1891 (Sarawak) with the last whorl more narrowly rounded around the periphery; Lamprocystis ambonica O Boettger, 1891 (Indonesia, Maluku) with a larger aperture. Sitala amussitata E A Smith, 1895 (Sarawak), and Lamprocystis subglobosa Von Möllendorff, 1897 (Indonesia, Java), see Van Benthem Jutting (1950: 452) have slightly laterally compressed whorls, resulting in a somewhat shouldered last whorl.

Variability. Juveniles and some adults have the basal corner of the peristome more angular than in the illustrated specimen. A small callus (not protruding beyond the rim of the peristome, as in *Microcystina appendiculata*) may be present on the columellar peristome in such shells. Shells from mount Kinabalu tend to be relatively small, with a distinctly elevated spire.

Microcystina sinica Von Möllendorff, 1885

(fig. 99g-j, 100c, map 20b)

Von Möllendorff 1885: 386; Maassen 1997: 62; Vermeulen & Whitten 1998: 118, 156; Maassen 2001: 112;

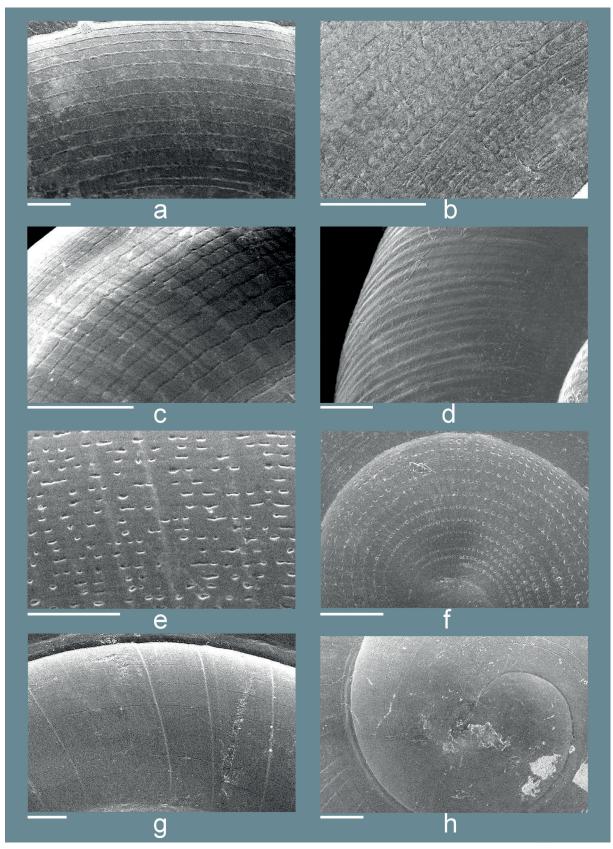


Fig. 100, a. *Microcystina callifera* Vermeulen, Liew & Schilthuizen, 2015, upper surface of the third whorl; b. *Microcystina striatula* Vermeulen, Liew & Schilthuizen, 2015, upper surface of the third whorl; c. *Microcystina sinica* Von Möllendorff, 1885, upper surface of the third whorl; d. *Microcystina consobrina* Van Benthem Jutting, 1959, upper surface of the third whorl; e–f. *Microcystina muscorum* Van Benthem Jutting, 1959, e. Upper surface of the third whorl, f. apex; g–h. *Microcystina gratilla* Van Benthem Jutting, 1950, g. Upper surface of the third whorl, h. Apex. All scale bars are 0.05 mm.

Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 46; Phung et al. 2017: 75; Foon et al. 2018: 95. – Type from China, Guangdong Prov., Shiu Heng Hap.

Cross diagnosis. Shares the small size, slowly expanding whorls, and pitted protoconch with *Microcystina muscorum*; it differs by having a continuous spiral striation on the teleoconch. Shells entirely without spiral striation can be distinguished by the color, as well as by the absence of shallow, widely spaced radial grooves, as occur in *M. muscorum*. *Microcystina striatula* and *M. gratilla* have more rapidly expanding whorls (diameter of third whorl 1.2–1.6 mm, versus 0.8–1.3 mm) and a flatter shell; *M. striatula* also has a white shell.

Description. Shell minute, thin, somewhat translucent, pale yellowish to pale corneous. Surface moderately glossy, or with a silky shine. Outline lenticular; spire moderately elevated, conical with a rounded apex. Whorls moderately convex. Sculpture. Protoconch sometimes with traces of radial riblets (barely visible at 40x magnification); with a fine, moderately spaced spiral striation consisting of rows of minute pits (barely visible at 40x magnification) which are arranged in a reticulate pattern. Teleoconch. Radial sculpture: Inconspicuous growth lines, next to these inconspicuous to distinct, well-spaced to densely placed shallow grooves, often at uneven intervals. Spiral sculpture sometimes approx. absent, usually very fine (just visible at 40x magnification), rather widely spaced, continuous, shallow, rather sharply outlined grooves present locally or over the entire shell. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus closed, or open and very narrow; columellar side of the peristome somewhat thickened but not covering the umbilicus; umbilical region slightly concave. Dimensions. Height up to 1.1 mm; width up to 1.7 mm; diameters of the first three whorls 0.3–0.5 mm, 0.5–0.8 mm, 0.8–1.3 mm respectively; number of whorls up to 4 1/8; height and width aperture up to 0.9 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2600 m. In primary and secondary forest, coastal woodland. Elsewhere also in more severely degraded environments such as *Imperata* grass fields. On limestone, sandstone/shale and volcanic bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Widespread, from S China to Indonesia (Java to West Papua).

Genus *Vitrinula* Gray, 1857 (= *Medyla* Albers, 1860) (= *Xesta* auct.)

Diagnosis for the Sabah species. Shell calcareous, with one or several spiral bands of distinctly different color, or shell without such bands. Shell above the periphery shiny or glossy, with or without an even sculpture, but without wrinkles and dents. Shell width in adults of 4–5 whorls 17.8–27.0 mm; ratio height/width 0.50–0.76. Umbilicus open, narrow, without spur protruding from the columellar corner.

Notes. Living *Vitrinula* differs from *Everettia* (Dyakiidae) by the presence of a finger-shaped lobe on the mantle edge. The shells of most *Vitrinula* species differ from *Everettia* by the coloration; *V. padasensis*, without any color bands, generally has a higher ratio height/width: 0.70–0.71, versus 0.49–0.68, with as additional character its approx. smooth shell (shell with a fine but conspicuous sculpture in *Everettia* species with a ratio height/width of 0.65–0.68.

KEY TO THE GROUPS

1 – Shell above the periphery with a colored band, well away from the suture

- Group 1
- 1- Shell above the periphery colored up to the suture, or shell without any coloration

Group 2

Group 1

Vitrinula baramensis (Kobelt, 1897)

(fig. 96f, 101a–c, map 20c)

Xesta baramensis Kobelt 1897: 52. - Type from Malaysia, Sarawak, 'Baram river'.

Description. Shell dextral, medium-sized, slightly translucent to opaque, white to green-corneous, with a narrow (distinctly narrower than de unpigmented band above it), (red-)brown band just above the periphery. Surface shiny. Spire depressed-conical with straight sides, apex narrowly rounded. Whorls moderately convex, last whorl evenly rounded (slightly more narrowly rounded at the periphery in juveniles). Sculpture. Protoconch smooth, with or without slight crenulations just below the suture. Teleoconch. Radial sculpture: Weak growth lines, slightly raised at uneven intervals, in some shells at approx. even intervals, creating a slightly wavy surface just below the suture in the outer whorls. Spiral sculpture above the periphery virtually absent, below the periphery often (locally) with (traces of) very fine (visible at 40x magnification) densely placed, very shallow grooves. Aperture broadly crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading.

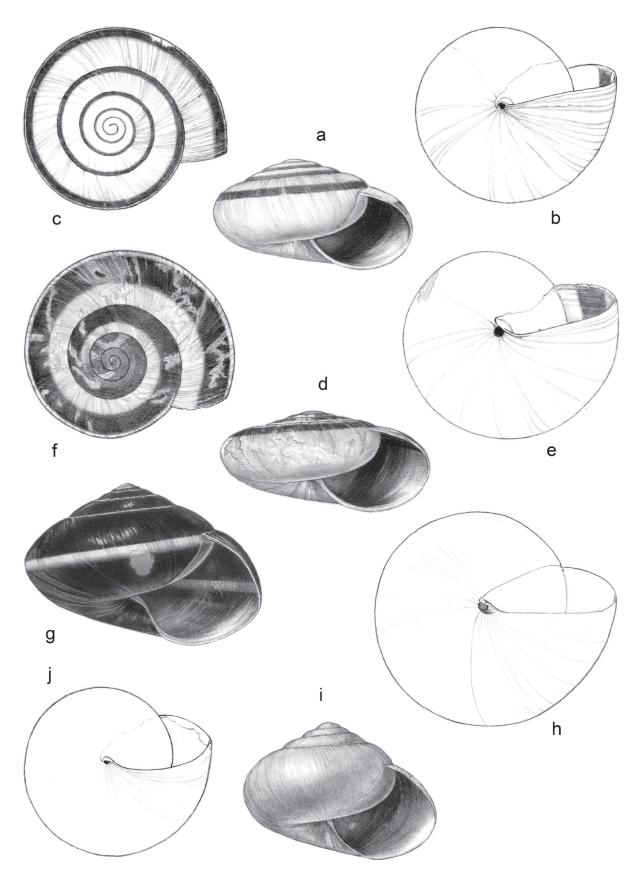


Fig. 101, a–c. *Vitrinula baramensis* (Kobelt, 1897), a. Frontal view, shell 10 mm high, b. Umbilical view, c. Apical view; d–f. *Vitrinula discus* Vermeulen & Liew, new species, d. Frontal view, shell 10 mm high, e. Umbilical view, f. Apical view; g–h. *Vitrinula decrespignyi* (Higgins, 1868), g. Frontal view, shell 17 mm high, h. Umbilical view; i–j. *Vitrinula padasensis* (E A Smith, 1895), i. Frontal view, shell 12.6 mm high, j. Umbilical view.

Umbilicus open, very narrow. Dimensions. Height up to 12(-17) mm; width up to 22(-27) mm; ratio height/width 0.53-0.58(-0.63); diameter of the first three whorls 1.7-2.0 mm, 3.1-4.1 mm, 6.1-7.5 mm respectively; umbilicus up to 0.8 mm diam., or 1-4 % of the shell width; number of whorls 4 1/4-4 3/4; height aperture up to 8.3 mm; width aperture up to 12 mm.

Distribution in Sabah. Widespread, scattered localities. Elevation range: 100–2200 m. In (disturbed) primary forest and secondary forest on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Variability. The type material is larger, shell measurements as in Kobelt (1897) are added between brackets.

Vitrinula discus Vermeulen & Liew, new species

(fig. 101d–f, map 20d)

Type specimens from Malaysia, Sabah, Tawau Prov., Danum valley Conservation Area (holotype BOR/MOL 944); Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (paratype JV 7505/1 shell). *Everettia* 'spec. banded' Schilthuizen et al. 2003b: 42.

Cross diagnosis. Differs from *Vitrinula baramensis* by the wide (as wide as or wider than de unpigmented band above it) dark band just above the periphery, and the inconspicuous (just visible at 20x magnification), shallow granulation present below the periphery.

Description. Shell dextral, medium-sized, approx. opaque, white to pale yellow-corneous, with a wide (as wide as or wider than de unpigmented band above it) red-brown band just above the periphery. Surface shiny above, a little duller below. Spire slightly raised to depressed-conical with approx. straight sides, apex narrowly rounded. Whorls slightly to moderately convex above the periphery, last whorl slightly more convex below, periphery slightly narrowly rounded (more so in juveniles). Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak growth lines, slightly raised at uneven intervals. Spiral sculpture: In some shells locally traces of very fine (barely visible at 40x magnification), shallow spiral striation. Next to this, an inconspicuous (just visible at 20x magnification), shallow granulation present below the periphery. Aperture broadly crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, very narrow. Dimensions. Height up to 12 mm; width up to 22 mm; ratio height/width 0.50–0.56; diameter of the first three whorls 1.8–2.5 mm, 3.4–4.8 mm, 7.3–8.8 mm respectively; umbilicus up to 1.6 mm diam., or 5–8 % of the shell width; number of whorls 3 7/8–4 7/8; height aperture up to 8.5 mm; width aperture up to 11.4 mm.

Distribution in Sabah. Scattered localities in E; elsewhere in Sapulut only. Elevation range: 0–400 m. In (disturbed) primary forest, also in secondary forest and in degraded, low shrubland. On limestone bedrock. Also in Kalimantan. Endemic to Borneo.

Similar species elsewhere. Nanina moluensis E A Smith, 1893, from adjacent Sarawak, also has a minutely granulose lower surface of the shell but differs by the more evenly rounded periphery and the moderately convex whorls above it

Name derivation. From δίσκος (Ancient Greek) = disk, used as a noun in apposition.

Group 2

Vitrinula decrespignyi (Higgins, 1868)

(fig. 96g, 101g-h, map 20c)

Clements et al. 2008: 2761. – Nanina (Xesta) decrespignyi Higgins 1868: 179 ('de-crespignii'); Issel 1874: 392; Pfeiffer & Clessin 1881: 39 ('crespignyi'); Tenison Woods 1888: 1014 ('crespignyi'); Aldrich 1889: 24. – Nanina decrespignyi (Higgins) Pfeiffer 1877 (1877–1880): 543 ('crespignyi') – Xesta decrespignyi (Higgins) Godwin-Austen 1891: 26; Von Martens 1908: 260 ('crespignyi'). – Medyla decrespignyi Vermeulen et al. 2007: 217. – Holotype from Malaysia, Labuan.

Cross diagnosis. Among Sabah Vitrinula identified by the very glossy, dark-colored shell.

Description. Shell dextral, large, translucent, dark red-brown except for a rather narrow peripheral band. Surface highly glossy. Spire depressed conical with convex sides, apex narrowly rounded. Whorls slightly convex above the periphery, the last narrowly rounded (obtusely angular in juveniles and often in sub-adults) at the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak growth lines, slightly raised at uneven intervals. Spiral sculpture absent, or below the periphery with a few unevenly spaced, very shallow grooves. Aperture broadly crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, very narrow. Dimensions. Height up to 19.0 mm; width up to 27.0 mm; ratio height/width 0.65–0.76; diameter of the first three whorls 2.0–3.0 mm, 4.5–6.0 mm, 8.2–11.0 mm respectively; umbilicus up to c. 1.0 mm diam., or c. 4 % of the shell width; number of whorls 4 7/8–5 1/4; height aperture up to 12.0 mm; width aperture up to 16.5 mm.

Distribution in Sabah. Widespread but rare and not found in recent years: Labuan, Terusan (old records).

Elevation range: 0–100 m. Elsewhere in rainforest on limestone bedrock. Also in Sarawak, Kalimantan (widely scattered localities). Endemic to Borneo.

Note. The spelling 'decrespignyi' has been in 'in prevailing usage' since 1889 (used 4 times, versus 1 time 'crespignyi' in 1908) and is therefore retained (ICZN art. 33.2.3.1).

Vitrinula padasensis (E A Smith, 1895)

(fig. 96h, 101i–j, map 20e)

Schilthuizen & Rutjes 2001: 421. – *Xesta padasensis* Smith 1895: 100; Von Martens 1908: 260. – Type from Malaysia, Sabah, upper Padas river valley.

Vitrinula 'unidentified' Schilthuizen 2004: 94.

Helicarion 'unidentified' Schilthuizen 2004: 95.

Cross diagnosis. Differs from *Vitrinula decrespignyi* by its pale shell, without a peripheral band of different color. Also, the shell is more evenly rounded at the periphery. *Helicarion dyakana* has a smaller 1st whorl, while the next whorls expand more rapidly (diameter of the 1st and the 4th whorls: 1.0–1.4 mm and 9.5–9.8 mm, versus 2.1–2.2 mm and 12.8–14.0 mm respectively).

Description. Shell dextral, medium-sized, translucent, uniformly pink-corneous to yellow-corneous. Surface highly glossy. Spire depressed-conical with approx. straight sides; apex rounded. Whorls slightly convex, the last approx. evenly rounded at the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Weak growth lines, slightly raised at uneven intervals. Spiral sculpture: Locally with inconspicuous, unevenly spaced, very shallow grooves. Aperture broadly crescent-shaped, basal peristome only slightly curved towards the columellar corner. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, very narrow. Dimensions. Height up to 12.6 mm; width up to 17.8 mm; ratio height/width 0.70–0.71; diameter of the first four whorls 2.1–2.2 mm, 4.0–4.6 mm, 7.2–8.6 mm, 12.8–14.0 mm respectively; number of whorls up to 4 5/8; umbilicus c. 0.8 mm diam., or c. 5 % of the shell width; height aperture up to 9.0 mm; width aperture up to 9.8 mm.

Distribution in Sabah. Rare in W: Kiansom, Crocker range, mount Lumaku, upper Padas valley (old record), Sapulut. Elevation range: 200–1200 m. In primary and secondary forest, on limestone and sandstone/shale bedrock. Endemic to Sabah.

The semi-slugs (Animal not fully retractable in its shell. Shell largely or entirely covered by the animal when creeping)

Note. In all genera the whorls of the calcareous part of the shell are open on the lower side because the inner shell walls are reduced to a low rim following the suture. The periostracum expands widely beyond the edge of the calcareous layer on the parietal, columellar and basal side of the aperture, has largely closed whorls and envelops the visceral mass.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Shell with c. 3 3/4 whorls. Shell with fine spiral sculpture Genus *Durgella* (see under the ariophantid snails)
- 1 Shell with up to 1 3/4 whorls. Shell without spiral sculpture
 - 2 Mantle entirely covering the shell, without a lumen

Genus Philippinella

- 2 Mantle with a lumen through which the shell can be seen
 - 3 Lumen in the mantle crescent-shaped; mantle-edge on the right side with a large circular lobe

Genus Ibycus

- 3 Lumen in the mantle approx. linear or elliptic; mantle-edge on the right side without a lobe
 - 4 Shell with 1–1 5/8 whorl. Penis proximally with a loop. Vas deferens connected to the apex of the epiphallus Genus *Microparmarion*
 - 4 Shell with c. 1/4 whorl or less. Penis proximally without a loop. Vas deferens connected close to the base of the epiphallus Genus *Parmarion*

Genus Ibycus Heynemann, 1863

Diagnosis for the Sabah species. Shell thinly calcareous, with periostracum. Calcareous layer shield-shaped, slightly concave, elliptic, with up to 1 3/8 rapidly expanding whorls which are open to the apex because the inner shell walls are reduced to a low rim following the suture.

Animal. Shell visible through a left-lateral, crescent-shaped lumen in the mantle; mantle-edge on the right side with a large circular lobe.

Anatomy. Penis proximally without a loop. Vas deferens inserted near the base of the epiphallus.

Notes. 1. Unidentified records in literature: Ibycus sp. Laidlaw 1937: 184.

2. Placed in Helicarionidae in MolluscaBase (accessed 1/2021).

Ibycus rachelae Schilthuizen & Liew 2008

(fig. 102a–d, 106a, map 20f)

Schilthuizen & Liew 2008: 296; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, mount Kinabalu.

Description. Shell approx. elliptic in outline. Radial sculpture: inconspicuous growth lines. Dimensions. Longest axis up to 13 mm; perpendicular to this up to 9.5 mm; ratio height/width 1.3–1.4; number of whorls approx. 1 3/8.

Animal (rather) large, slender; tail long. Mantle rather finely to coarsely, densely and evenly papillose. Color greyish to white, anterior part of the body with 2 usually rather inconspicuous, wide longitudinal dark lines starting at the foot of the tentacles, median ridge on the tail bright yellow or green; wrinkles at the base of the tentacles, on the posterior part of the body, and the papillae on the mantle iridescent green. Dimensions. Body up to 40 mm long.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range. Elevation range: 1000–2000 m. Primary forest on sandstone/shale bedrock. Endemic to Sabah.

Genus Microparmarion Simroth, 1893

Diagnosis for the Sabah species. Shell thinly calcareous, with periostracum. Calcareous layer shield-shaped, slightly concave, elliptic, with up to 1 1/2 rapidly expanding whorls which are open to the apex because the inner shell walls are reduced to a low rim following the suture.

Animal. Shell visible through a straight, median or left-lateral lumen in the mantle; mantle-edge on the right side without a lobe.

Anatomy. Penis proximally with a loop: Transition of penis to epiphallus bent upon itself and, just below the epiphallus, attached to the penis through an extension the muscular tube around the penis. Vas deferens connected to the apex of the epiphallus.

Notes. Unidentified records in literature:

Microparmarion sp. Laidlaw 1937: 184.

Microparmarion aff. M. pollonerai Schilthuizen & Liew 2008: 297, sub M. pollonerai.

Microparmarion sp. Schilthuizen & Liew 2008: 299.

KEY TO THE GROUPS

- 1 Part of mantle surrounding the shell with 1–2 peripheral ridges, (the longest) from the left anterior side of the shell, along the posterior edge where it is narrowly interrupted, to the right posterior side. Looped part of the penis tapering to a thin tube, approximating the vas deferens in thickness, towards the epiphallus **Group 1**
- 1 Part of mantle surrounding the shell without a peripheral ridge. Looped part of the penis somewhat tapering or not towards the epiphallus, but much thicker than the vas deferens

 Group 2

Group 1

Microparmarion exquadratus Schilthuizen et al. 2019

(fig. 102e, 106c, map 21a)

Schilthuizen et al. 2019: 36. – Type from Malaysia, Sabah, Tawau Hills.

Cross diagnosis. Differs from *Microparmarion pollonerai* by the presence of a single peripheral ridge on the mantle, on the right side of the animal. Also, it is distinctly smaller (body 18–21 mm long, versus c. 40 mm long).

Description. Shell approx. elliptic in outline. Radial sculpture: a few inconspicuous growth lines. Dimensions. Longest axis up to 9 mm; perpendicular to this up to 5 mm; ratio height/width 1.7–1.8; number of whorls c. 1 1/8.

Animal rather small, rather sturdy; tail rather short. Mantle distinctly rugulose; part surrounding the shell with 1 peripheral ridge from the left anterior side of the shell, along the posterior edge where it is narrowly interrupted, to the right posterior side, where it ends well behind the respiratory pore. Color dull orange to pale red with dark brown pattern: Tentacles often dark, anterior part of body with 3 distinct, wide longitudinal lines, the lateral ones starting at the foot of the tentacles, posterior part with 1 longitudinal line, sides with spots, foot margin with minute vertical markings; mantle with an uneven, wide, locally interrupted dark ring surrounding the lumen, otherwise coarsely spotted. Dimensions. Body 18–21 mm long.

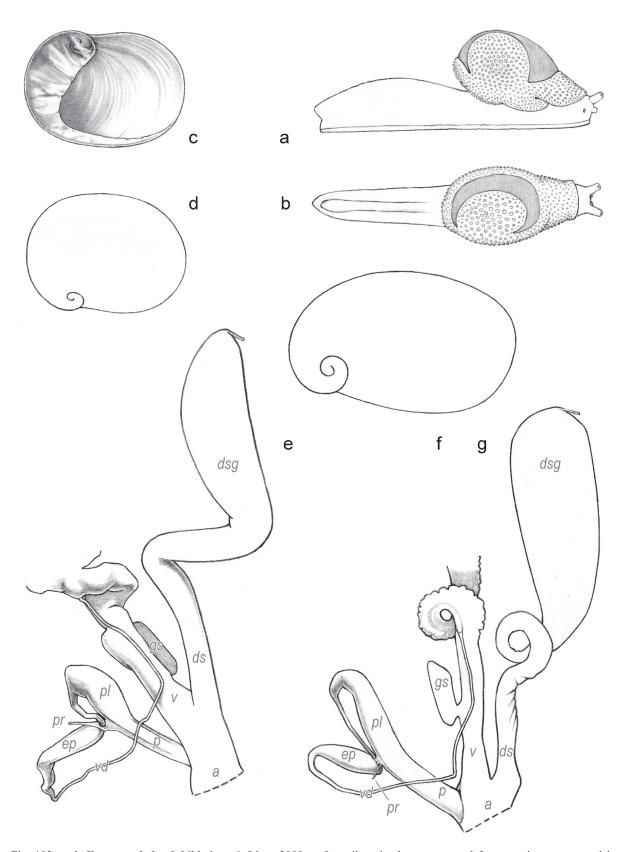


Fig. 102, a–d. *Ibycus rachelae* Schilthuizen & Liew, 2008, a. Juvenile animal, reconstructed from specimen preserved in alcohol, right lateral view, animal 19 mm long, b. Dorsal view, c. Shell, umbilical view, shell 6 mm wide, d. Apical view; e. *Microparmarion exquadratus* Schilthuizen et al., 2019, distal part of genitals, dart sac as drawn 11.5 mm long; f–g. *Microparmarion pollonerai* Collinge & Godwin-Austen, 1895, f. Shell, apical view, g. Distal part of genitals. Abbreviations: a = atrium; ds = dart sac; dsg = dart sac gland; ep = epiphallus; gs = gametolytic sac; p = penis; pl = looped part of the penis; pr = penis retractor muscle; v = vagina; vd = vas deferens.

Anatomy. Looped part of the penis tapering to a thin tube, much thinner than the penis itself, towards the epiphallus.

Distribution in Sabah. Widespread but rare: Mount Lumaku, Tawau hills. Elevation range: 400–500 m. Lowland dipterocarp forest. Endemic to Sabah.

Microparmarion pollonerai Collinge & Godwin-Austen, 1895 (fig

(fig. 102f–g, 106d, map 21a)

Collinge & Godwin-Austen 1895: 244; Godwin-Austen 1898 (1897–1914): 55; Laidlaw 1937: 180; Vermeulen 1996b: 286; Schilthuizen & Liew 2008: 297; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Collingea pollonerai* (Collinge & Godwin-Austen) Von Martens 1908: 259. – Type from Borneo, Sabah, mount Kinabalu.

[Not Microparmarion pollonerai auct. Hoffmann 1943: 78; =? Microparmarion convolutus].

Cross diagnosis. Characterized by the presence of 2 ridges on the mantle part surrounding the shell: 1 peripheral ridge, and 1 much shorter subperipheral ridge on the right posterior side.

Description. Shell approx. elliptic in outline. Radial sculpture: a few inconspicuous growth lines. Dimensions. Longest axis up to 16 mm; perpendicular to this up to 10 mm; ratio height/width c. 1.6; number of whorls c. 1 5/8.

Animal medium-sized, rather sturdy; tail rather short. Mantle approx. smooth; part surrounding the shell with 2 ridges: 1 peripheral ridge from the left anterior side of the shell, along the posterior side where it is narrowly interrupted, to the right anterior side of the shell, 1 subperipheral, shorter ridge on the right posterior side. Color grey-brown to red-brown on the back, yellow-green on the tail, without dark longitudinal lines, sides a paler brown towards the foot. Dimensions. Body c. 40 mm long.

Anatomy. Looped part of the penis tapering to a thin tube, much thinner than the penis itself, towards the epiphallus.

Distribution in Sabah. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 1900–3400 m. Damp primary forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Group 2

Microparmarion basifixus Vermeulen & Liew, new species

(fig. 103a–f, map 21b)

Type from Malaysia, Sabah, Crocker Range N.P., Ulu Kimanis (holotype BOR/MOL 14840).

(?) Microparmarion 'unidentified' Schilthuizen 2004: 95.

Collingea smithi auct. Collinge 1901: 304. – Microparmarion smithi auct. Hoffmann 1943: 83.

[Not Damayantia smithi Collinge & Godwin-Austen].

Cross diagnosis. Differs from *Microparmarion convolutus* by the larger and wider body (body length 27–30 mm versus 18–20 mm in spirit preserved specimens), and by the presence of scattered, large, flat tubercles on the posterior surface of the mantle.

Description. Shell approx. elliptic in outline. Radial sculpture: a few inconspicuous growth lines. Dimensions. Longest axis up to 14 mm; perpendicular to this up to 11 mm; ratio height/width 1.25–1.7; number of whorls 1–1 1/4

Animal medium-sized, rather sturdy; tail rather short. Mantle minutely and rather inconspicuously papillose; part covering the posterior edge of the shell also with scattered, large, flat tubercles. Color (spirit preserved material) pale with a dark pattern: Anterior part of body with 3 somewhat vaguely outlined longitudinal lines, the lateral ones starting at the foot of the tentacles, posterior part without longitudinal lines; anterior part of the mantle vaguely mottled. Dimensions. Body 27–30 mm long (spirit preserved material).

Anatomy. Looped part of the penis not or hardly tapering towards the epiphallus; both legs of the loop connected to the penis just below the epiphallus.

Distribution in Sabah. Highlands: Crocker range, Trus Madi range. Elevation range: 600–1900 m. Damp primary forest on sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Microparmarion hildegardi Hoffmann, 1934 (from Sumatra) shares the papillose mantle surface but has the looped part of the penis more distinctly tapering towards the epiphallus (though not as much as in the species of Group 1).

Name derivation. From basis (Latin) = base, and fixus = attached to, referring to the looped part of the penis near the basis of the epiphallus.

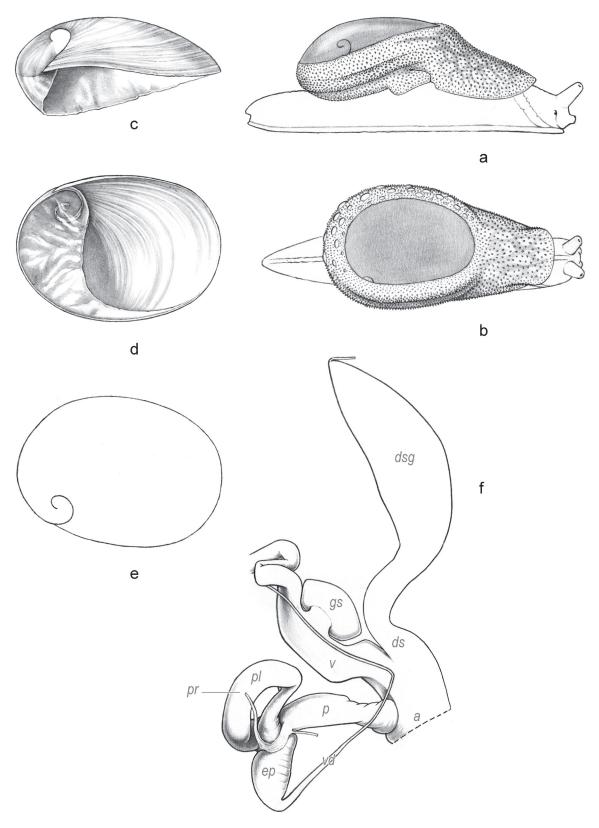


Fig. 103, a–f. *Microparmarion basifixus* Vermeulen & Liew, new species, a. Animal, reconstructed from specimen preserved in alcohol, right lateral view, animal 30 mm long, b. Dorsal view, c. Shell, frontal view, shell 13.4 mm wide, d. Umbilical view, e. Apical view, f. Distal part of genitals, dart sac 14.5 mm long. Abbreviations: a = atrium; ds = dart sac; dsg = dart sac gland; ep = epiphallus; gs = gametolytic sac; p = penis; pl = looped part of the penis; pr = penis retractor muscle; v = vagina; vd = vas deferens.

Microparmarion convolutus Vermeulen & Liew, new species

(fig. 104a–g, 106b, map 21c)

Type from Malaysia, Sabah, Crocker Range N.P., Mahua falls (holotype BOR/MOL 14841; paratype JV 9724/1 animal).

(?) Microparmarion pollonerai auct. Hoffmann 1943: 78.

[Not Microparmarion pollonerai Collinge & Godwin-Austen].

Cross diagnosis. Differs from *Microparmarion basifixus* by the smaller and slenderer body (body length 18–20 mm versus 27–30 mm in spirit preserved specimens), and by the absence of scattered tubercles on the posterior surface of the mantle.

Description. Shell approx. elliptic in outline. Radial sculpture: a few inconspicuous growth lines. Dimensions. Longest axis up to 8 mm; perpendicular to this up to 5.3 mm; ratio height/width c. 1.5; number of whorls c. 1 1/4.

Animal rather small, slender; tail rather short. Mantle approx. smooth. Color whitish, pale orange or pale pink with a slight greyish mottling on the sides and the tail; anterior part of body with 2–3 distinct, wide longitudinal dark brown or black lines, the lateral ones starting at the foot of the tentacles; posterior part without longitudinal lines: mantle brown with pale spots, or pale, with an uneven, interrupted dark ring surrounding the lumen, anterior part stained or marbled, less distinctly so towards the edges. Dimensions. Body 18–20 mm long (spirit preserved material).

Anatomy. Looped part of the penis not or hardly tapering towards the epiphallus; both legs of the loop connected to the penis just below the epiphallus.

Distribution in Sabah. Crocker range only. Elevation range: 1100–1200 m. Damp primary forest on sandstone/shale bedrock. Endemic to Sabah.

Name derivation. From convolutus (Latin) = rolled up, referring to the shape of the looped part of the penis.

Microparmarion simrothi Collinge & Godwin-Austen, 1895

(fig. 104h–i, 106e, map 21d)

Collinge & Godwin-Austen 1895: 246; Godwin-Austen 1898 (1897–1914): 58; Laidlaw 1937: 183; Hoffmann 1943: 82 (in syn.); Vermeulen 1996b: 286; Schilthuizen & Liew 2008: 299; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Collingea simrothi* (Collinge & Godwin-Austen) Von Martens 1908: 259. – Type from Borneo, Sabah, mount Kinabalu.

Cross diagnosis. Differs from Microparmarion basifixus and M. convolutus by the larger whorl count of the shell (approx. 1 5/8 whorls versus 1–1 1/4 whorls). It differs also by the coarsely papillose mantle with at least some acute papillae. Anatomically, it differs by the looped part of the penis, with one leg of the loop connecting with the penis just below the epiphallus, and the other approx. half-way along the length of the epiphallus (versus both legs connecting with the penis just below the epiphallus).

Description. Shell elliptic to ovate in outline. Radial sculpture consisting of distinct growth lines. Dimensions. Longest axis up to 17 mm; perpendicular to this up to 14 mm; ratio height/width c. 1.2; number of whorls c. 1 5/8.

Animal medium-sized, rather sturdy; tail rather short. Mantle coarsely and distinctly papillose, with at least some acute papillae and with some larger papillae interspersed; part covering the edge of the shell also with scattered, large tubercles. Color pale yellow to light (ochre-)brown, with a dark pattern: Anterior part of body with 3 distinct, wide longitudinal lines, the lateral ones starting at the foot of the tentacles, posterior part with 1 longitudinal line, sometimes divided into two by a pale line along the median keel, sides with scattered large spots, foot margin with scattered vertical markings; mantle with an uneven, interrupted dark ring close to the periphery of the part covering the shell, and often with spots bordering the edges of the lumen, anterior part marbled to coarsely spotted. Dimensions. Body up to 45 mm long (spirit preserved material).

Anatomy. Looped part of the penis not or hardly tapering towards the epiphallus; one leg of the loop connected to the penis just below the epiphallus, the other approx. half-way along the length of the epiphallus.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 1300–3200 m. Primary forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Genus Parmarion Fischer, 1855

Diagnosis for the Sabah species. Shell (thinly) calcareous, with a periostracum. Calcareous layer shield-shaped, slightly concave, elliptic, approx. without whorls or with at most 1/4 rapidly expanding whorl which is open to the apex because the inner shell walls are reduced to a low rim following the suture.

Animal. Shell visible through a straight, median or left-lateral lumen in the mantle. Mantle-edge on the right side without a lobe.

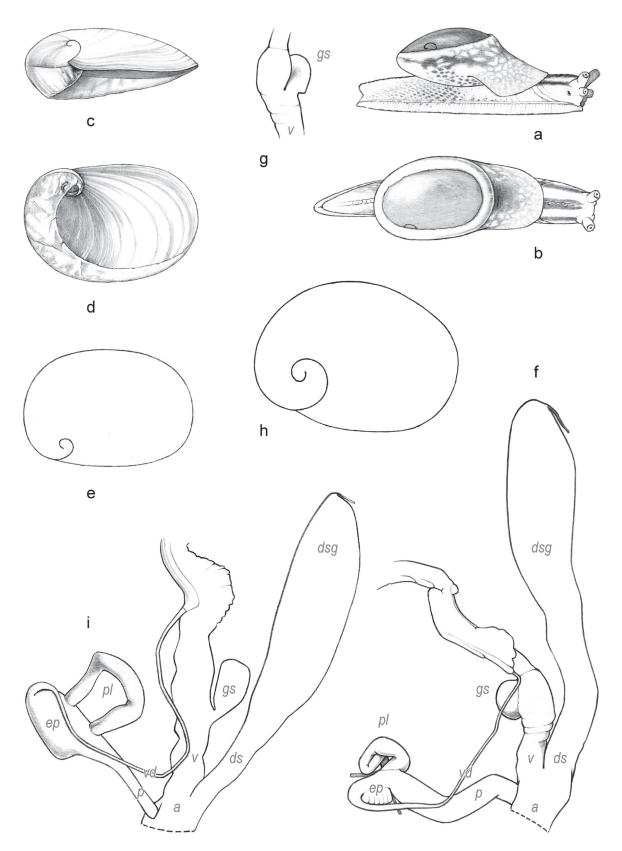


Fig. 104, a–g. *Microparmarion convolutus* Vermeulen & Liew, new species, a. Animal, reconstructed from specimen preserved in alcohol, right lateral view, animal 17 mm long, b. Dorsal view, c. Shell, frontal view, shell 8 mm wide, d. Umbilical view, e. Apical view, f. Distal part of genitals, dart sac as drawn 6.5 mm long, g. Receptaculum seminis; h–i. *Microparmarion simrothi* Collinge & Godwin-Austen, 1895, h. Shell, apical view, i. Distal part of genitals. Abbreviations: a = atrium; ds = dart sac; dsg = dart sac gland; ep = epiphallus; gs = gametolytic sac; p = penis; pl = looped part of the penis; v = vagina; vd = vas deferens.

Anatomy. Penis proximally without a loop. Vas deferens connected close to the base of the epiphallus.

Notes. Unidentified records in literature:

Parmarion sp. Clements et al. 2008: 2761; Schilthuizen & Liew 2008: 300.

Parmarion martensi Simroth, 1893

(fig. 105a–d, 106f, map 21e)

Simroth 1893 (1893–1894): 107; Hoffmann 1943: 32; Van Benthem Jutting 1950: 438; 1959: 159; Cowie 1997: 16; Maassen 2001: 108; Schilthuizen & Liew 2008: 299; Tan et al. 2012: 115. – Type from Cambodia.

Description. Shell approx. elliptic in outline. Radial sculpture consisting of inconspicuous growth lines. Dimensions. Longest axis up to 15 mm; perpendicular to this up to 11 mm; ratio height/width 1.3–1.5; number of whorls approx. 1/4 or less.

Animal (rather) large, rather slender; tail rather long. Mantle minutely wrinkled; part surrounding the shell with 1 peripheral ridge from the left anterior side of the shell, along the posterior edge where it is narrowly interrupted, to the right side, where it ends close to the respiratory pore. Color pink to pale grey-brown, with a darker pattern: Tentacles dark, anterior part of body with 2 usually rather distinct, wide longitudinal lines, starting at the foot of the tentacles, posterior part with 2 similar longitudinal lines with a pale or white median keel in between, sides without pattern or with a slight marbling, foot margin with or without vertical markings; mantle with or without a slightly darker marbling, ridges pale or white. Entirely blackish animals, with patterns in a deeper black, also occur. Dimensions. Body up to 90 mm long, but specimens of 40 mm can also be mature.

Distribution in Sabah. Widespread, rare but probably under-recorded: Kota Kinabalu, Crocker range, lower Kinabatangan. Elevation range: 0–1800 m. In disturbed vegetation around human habitation, but also in primary forest. On sandstone/shale bedrock. Also in Kalimantan. Distribution elsewhere: Vietnam, Cambodia, Laos, Malaysia (Peninsula), Indonesia (Sumatra, Java), E-wards to the Pacific.

Notes. 1. Introduced in Sabah according to Schilthuizen et al. (2008: 299), because mainly found in degraded environments. We have one record from primary forest at 1800 m alt.

2. On external characters alone, *Parmarion martensi* cannot be distinguished with certainty from *P. pupillaris* Humbert, 1864. The latter might occur in Sabah; the two differ by the shape of the dart; fig. 106d and e show the darts of both species.

Genus Philippinella Von Möllendorff, 1899

Diagnosis for the Sabah species. Shell thinly calcareous, with a periostracum. Calcareous layer shield-shaped, approx. flat, elliptic, without whorls.

Animal. Shell not visible, mantle without lumen.

Anatomy. Penis proximally without a loop. Vas deferens inserted near the base of the epiphallus.

Philippinella moellendorffi Collinge, 1899

(fig. 105f–g, map 21f)

Collinge 1899: 55; Hoffmann 1943: 120; Schilthuizen & Liew 2008: 301. - Type from Philippines, Mindoro.

Description. Shell approx. elliptic in outline. Apex near the margin on the right side, close to the posterior end. Growth lines inconspicuous. Dimensions. Longest axis up to 7 mm; perpendicular to this up to 4.5 mm; ratio height/width 1.5–1.6.

Animal rather large, rather slender; tail rather short. Mantle minutely wrinkled; with 1 ridge well above the periphery, running from the left anterior side of the mantle to its posterior edge, along the posterior periphery of the mantle to the right side, where it ends close to the respiratory pore. Color (spirit preserved material) pale, with a darker pattern: Posterior part with almost longitudinal dark dashes on the sides, close to the foot; foot margin with vertical markings; mantle with scattered spots, less distinctly so towards the posterior end. Dimensions. Body up to 50 mm long (spirit preserved material).

Distribution in Sabah. Widespread but rare: Pulau Tiga Park, mount Kinabalu, Sepilok, lower Kinabatangan. Elevation range: 0–500 m. In degraded environments. Possibly introduced. Distribution elsewhere: Philippines.

Family **CAMAENIDAE** Pilsbry, 1895

(incl. BRADYBAENIDAE Pilsbry, 1898)

Diagnosis for the Sabah species. Snails. Shell with 3 3/8-7 1/8 slowly to rather rapidly expanding whorls.

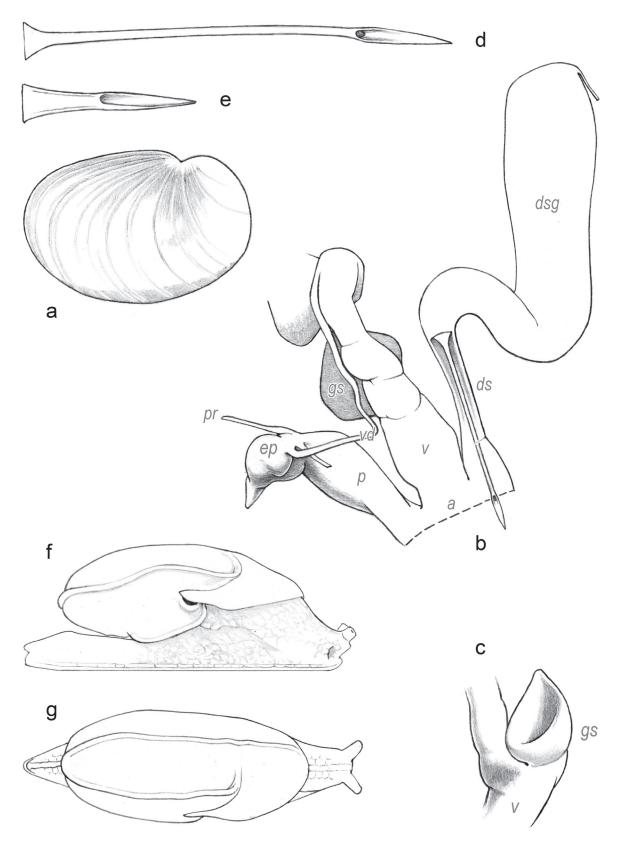


Fig. 105, a–d. *Parmarion martensi* Simroth, 1893, a. Shell, apical view, shell 13 mm wide, b. Distal part of genitals, dart sac as in drawing 11.5 mm long, c. Receptaculum seminis, d. Dart, 2.8 mm long; e. *Parmarion pupillaris* Humbert, 1864, dart, 1.7 mm long; f–g. *Philippinella moellendorffi* Collinge, 1899, f. Animal, right lateral view, g. Dorsal view. Abbreviations: a = atrium; ds = dart sac; dsg = dart sac gland; ep = epiphallus; gs = gametolytic sac; p = penis; pr = penis retractor muscle; v = vagina; vd = vas deferens.

Shell dextral or sinistral, medium-sized to large, higher than wide to wider than high; spire elongated conical to ovoid to depressed lenticular; last whorl rounded to acutely keeled at the periphery. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines (raised to riblets in *Landouria*); spiral sculpture absent or present, fine; next to this periostracal hair scars present in several genera, and/or a minute, dense granulose sculpture in some. Aperture without teeth (but with a tooth in *Obba moricandi*). Peristome on the palatal side thickened or not, spreading. Umbilicus closed to open and rather narrow (but rather wide in *Landouria*). Dimensions: Adults 7–53 mm high, 9–33 mm wide.

Notes. 1. Several genera have hairs on the periostracum, where these hairs are implanted the underlying shell surface shows a slight swelling (the periostracal hair scars).

2. Helix antiqua A Adams & Reeve, 1850, Helix borneensis L Pfeiffer, 1850, Helix germanus Reeve, 1852, Helix palawanica L Pfeiffer, 1855 (including Helix monochroa G B Sowerby I, 1841, Helix doriae Dohrn, 1881), and Helix trailli L Pfeiffer, 1855 are camaenid species (or species resembling Camaenidae) which are excluded from the Sabah fauna, see under Excluded Species.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Shell elongated conical, or ellipsoid or ovoid
 - 2 last whorl acutely keeled at the periphery

Genus Ganesella

- 2 last whorl rounded to obtusely angular at the periphery
 - 3 Diameter of the second whorl 6.0–8.8 mm. Periostracum greyish brown, dull, opaque (but easily wearing off). Shell dextral Genus *Cochlostyla*
 - 3 Diameter of the second whorl 5.5 mm or less. Periostracum absent or present, very thin, translucent. Shell dextral or sinistral Genus *Amphidromus*
- 1 Shell depressed conical, depressed globose or lenticular
 - 4 Shell surface with periostracal hair scars (sometimes distinct in the umbilical area only)
 - 5 Umbilicus open, 26–30 % of the shell width. Spiral sculpture present

Genus Landouria

- 5 Umbilicus closed or open, up to 19 % of the shell width. Spiral sculpture absent
 - 6 Either last half-whorl with its periphery distinctly above half-way its height, or aperture distinctly drawn-out into a beak on the palatal side

 Genus *Trachia*
 - 6 Last half-whorl with its periphery at approx. half-way its height or slightly above. Aperture not drawn-out into a beak on the palatal side Genus *Chloritis*
- 4 Shell surface without periostracal hair scars
 - 7 Last whorl distinctly descending towards the aperture; aperture at an angle of more than 60° with the coiling axis

 Genus *Obba*
 - 7 Last whorl slightly descending towards the aperture or not; aperture at an angle of 45° with the coiling axis or less
 - 8 Diameter of second whorl 2.2–2.8 mm

Genus Bradybaena

8 - Diameter of second whorl 9.6-10.3 mm

Genus Chloraea

Genus Amphidromus Albers, 1850

Diagnosis for the Sabah species. Shell dextral or sinistral, elongated conical, or ellipsoid or ovoid, (rather) large, last whorl rounded, slightly descending towards the aperture or not, its periphery at approx. half-way its height. Apex narrowly rounded. Spiral sculpture present or absent. Periostracum absent or very thin, deciduous, shiny, translucent; periostracal hair-scars on shell surface absent. Aperture at an angle of 30° to the coiling axis or less, not drawn-out on the palatal side. Umbilicus closed or open, very narrow. Diameter of second whorl 5.5 mm or less.

Notes. 1. The taxonomy of the genus is complicated, mainly because most species show extreme color variation, which has tempted authors to describe species where there may be none. We have not attempted to compare Borneo taxa with extralimital ones.

2. Amphidromus everetti var. connectens Fulton, 1896: See under Species of Uncertain Position.

KEY TO THE GROUPS

1 – Spire conical with almost straight sides

Group 1

1 – Spire conical with convex sides, or spire ellipsoid to ovoid

Group 2

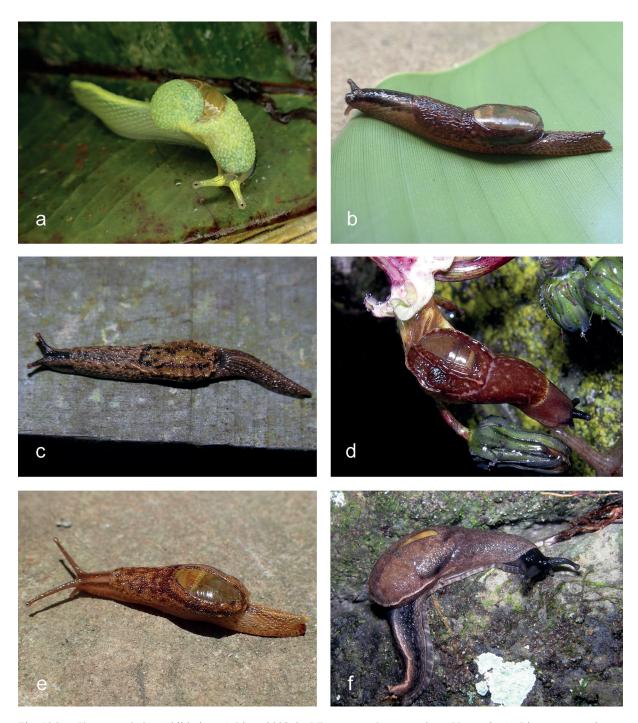


Fig. 106, a. *Ibycus rachelae* Schilthuizen & Liew, 2008; b. *Microparmarion convolutus* Vermeulen & Liew, new species; c. *Microparmarion exquadratus* Schilthuizen et al., 2019; d. *Microparmarion pollonerai* Collinge & Godwin-Austen, 1895; e. *Microparmarion simrothi* Collinge & Godwin-Austen, 1895, contracted animal; f. *Parmarion* cf. *martensi* Simroth, 1893.

Group 1

Amphidromus adamsii adamsii (Reeve, 1848)

(fig. 107a, 108a-b, 109a-e, map 22a)

Amphidromus adamsii (Reeve) Von Martens 1891 (1892): 241; Schepman 1896: 156; Fulton 1896: 82 (including varieties articulata, aureocincta, duplocincta, inornata, luteofasciata, ornata, rubiginosa, rufocincta, superba, simplex, subunicolor); Pilsbry 1900: 221 (including varieties articulata, aureocincta, duplocincta, inornata, luteofasciata, ornata, rubiginosa, rufocincta, superba, simplex, subunicolor); Von Martens 1908: 262;

Zilch 1953b: 131 (including varieties *aureocincta*, *luteofasciata*, *rubiginosa*); Laidlaw & Solem 1961: 579; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 80; Foon et al. 2018: 95. – *Bulimus adamsii* Reeve 1848 (1848–1850): Pl. 13, fig. 73; A Adams & Reeve 1850 (1848–1850): 58, pl. 15, fig. 1; Von Martens 1867: 356; Issel 1874: 312. – *Cochlostyla (Amphidromus) adamsii* (Reeve) Pfeiffer & Clessin 1881: 214. – Type from Borneo, Sabah, 'islet between Banggi and Balambangan islands').

Amphidromus gossi Bartsch 1904 (1905): 292. – Type from Malaysia, Sabah, mount Kinabalu. [Not *Bulimus adamsii* Issel 1874: 49; = *Amphidromus hamatus*].

Cross diagnosis. Among Sabah Amphidromus characterized by the minute brown spot on the shell apex.

Description. Shell sinistral, large, thin, white to yellow to pale ochre (with a pink hue), or olive-green, with or without wide blue-purple spiral bands which are often so wide that they leave only narrow spaces in between, with 3–5 of these bands on the last whorl (the middle band may be divided into 2 or 3 bands), 2 on the other whorls (historical material includes shells with bands consisting of well-separated patches and shells with predominant radial color patterns); apex with a small brown spot. Spire elongated-conical with almost straight sides and narrowly rounded apex. Surface shiny. Whorls: Moderately convex, last whorl rounded, not or hardly protruding. Sculpture. Protoconch minutely rugulose, not punctate. Teleoconch. Radial sculpture: inconspicuous growth lines, slightly raised at uneven intervals. Spiral sculpture: Traces of some very fine, shallow striation, just visible at 40x magnification. Aperture inside with approx. the same colors as outside, peristome thin on the parietal side, elsewhere white or pale purple, not thickened, moderately spreading. Umbilicus closed. Dimensions. Height 23–38 mm; width 14–20 mm; ratio height/width 1.6–2.2; number of whorls 5 1/2–6 5/8, height aperture 10–19 mm; width aperture 8–13 mm.

Distribution in Sabah. Rather common on islands in N: Mantanani, Balambangan, Banggi and Malawali islands; possibly on mount Kinabalu (Bartsch 1904). Elevation range: 0–400 m, but the Kinabalu record from high montane conditions. Primary and secondary forest, coastal woodland on limestone and granodiorite bedrock. Distribution elsewhere: Philippines (? See also note below subsp. pictus).

Variability. Fulton (1896) describes and illustrates forms of subsp. adamsii from Banggi island which display a wide variety of purplish color patterns, including spiral bands broken into squarish rows of spots, or rows of axially arranged spots. The type of Amphidromus adamsii, too, has the peripheral purplish band broken into spots. However, in our present-day material from Banggi and Balambangan islands we find a much more limited variability: An un-interrupted spiral banding.

Note. Fulton also depicts forms of this species from 'North Borneo'; it is unclear if he means the mainland or if he uses it as a general term that includes the various offshore islands. We have not found subsp. *adamsii* in mainland Sabah; the only proof of its possible occurrence there is the type of *Amphidromus gossi*, found on mount Kinabalu at high altitude. This has a shell shape as subsp. *adamsii*, but with a color pattern reminiscent of subsp. *pictus*.

Amphidromus adamsii pictus (Fulton, 1896)

(fig. 107b, 108c–d, 109f–h, map 22a)

Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54. – *Amphidromus pictus* Fulton 1896: 85; Pilsbry 1900: 226; Von Martens 1908: 262; Laidlaw & Solem 1961: 649; Vermeulen 1996b: 287. – Type from Malaysia, Sabah, mount Kinabalu.

Amphidromus pictus var. concinnus Fulton 1896: 85; Pilsbry 1900: 226. – Type from Malaysia, Sabah, mount Kinabalu.

Cross diagnosis. Differs from the type subspecies by the absence of the minute brown spot on the shell apex. It differs also by the often slightly more protruding last whorl, and by having, on average, one more whorl.

Description. As the type subspecies but with or without blue-purple markings usually consisting of 2–3 spiral bands on the last whorl, the upper of which is situated slightly below the periphery, above this with radial or oblique markings (in few shells these continue down to the umbilicus, and the spiral bands are absent), apex not darker than the rest of the shell. Whorls: Last whorl often slightly protruding. Dimensions. Height 33–41 mm; width 17–21 mm; ratio height/width 1.8–2.3; number of whorls (6–)6 1/2–7 1/8, height aperture 13–18 mm; width aperture 9–13 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–1400 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Also in Sarawak, Kalimantan (E part). Distribution elsewhere: Philippines (?, see note).

Variability. Mantanani island (off the W coast of Sabah) shells are intermediate between the subspecies: They do not have the minute brown spot on the apex but a whorl count more fitting into subsp. adamsii (whorl count in

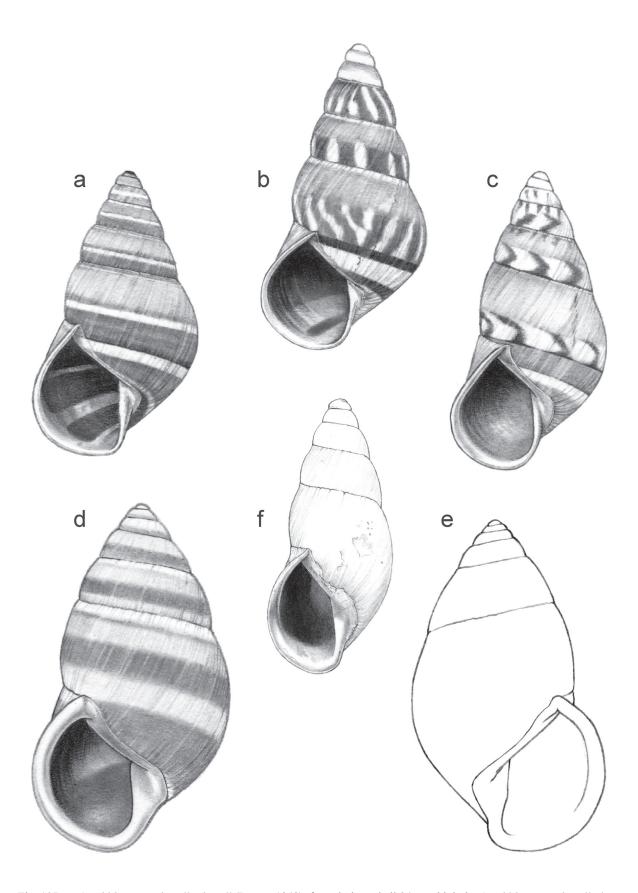


Fig. 107, a. *Amphidromus adamsii adamsii* (Reeve, 1848), frontal view, shell 34 mm high; b. *Amphidromus adamsii pictus* (Fulton, 1896), frontal view, shell 37 mm high; c. *Amphidromus hamatus* Fulton, 1896, frontal view, shell 29 mm high; d–e. *Amphidromus martensi* O Boettger, 1894, frontal views, d. Shell 46 mm high, e. Shell 44.5 mm high; f. *Amphidromus pse-phos* Vermeulen, Liew & Schilthuizen, 2015, frontal view, shell 24 mm high.

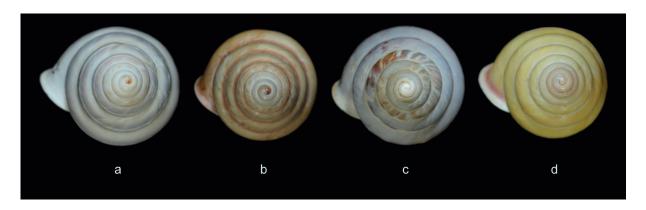


Fig. 108, a-b. *Amphidromus adamsii adamsii* (Reeve, 1848), apical views; c-d. *Amphidromus adamsii pictus* (Fulton, 1896), apical views

brackets in the description). They are also uniformly yellow, a color otherwise not represented in our Sabah material, although predominant in Kalimantan shells.

Note. Laidlaw and Solem (1961: 581) suggest this could be identical with *Amphidromus quadrasi* Hidalgo, 1887. The two are of similar shape, and Fulton (1896: 85) describes and illustrates a variability in colors and color patterns in *A. quadrasi* almost identical to that in *A. adamsii*.

Amphidromus hamatus Fulton, 1896

(fig. 107c, 110a-e, 117a, map 22b)

Fulton 1896: 84; Laidlaw & Solem 1961: 625. – *Amphidromus adamsii hamatus* (Fulton) Pilsbry 1900: 224. – Type from Malaysia, Labuan island.

Bulimus adamsii auct. Issel 1874: 412.

[Not Bulimus adamsii Reeve].

Cross diagnosis. Differs from *Amphidromus adamsii* by the not-rugulose but shallowly punctate protoconch. It also differs from subsp. *adamsii* by the apex without a minute brown spot, and from subsp. *pictus* by the generally smaller whorl count. Generally, *A. adamsii* differs by the more vivid color pattern on the shell (blue-purple in *A. adamsii*, versus a rather subdued brown in *A. hamatus*).

Description. Shell sinistral, large, thin, white to pale (lemon) yellow to pale ochre, below the periphery of somewhat brighter color than above, with or without (pale) brown markings: A narrow or wide spiral band at the periphery, above this with widely spaced oblique blotches which start at the periphery and then disappear or split into two thinner lines, below the periphery usually without markings or with two wide, paler brown spiral bands; apex not darker than the rest of the shell. Spire elongated-conical with almost straight sides and narrowly rounded apex. Surface shiny. Whorls: Moderately convex, last whorl rounded or slightly angular at the periphery. Sculpture. Protoconch shallowly punctate. Teleoconch. Radial sculpture: inconspicuous growth lines, slightly raised at uneven intervals. Spiral sculpture: Traces of very fine, shallow striation, just visible at 40x magnification. Aperture inside with approx. the same colors as outside, peristome thin on the parietal side, elsewhere not thickened, slightly spreading, white or pale pink-purple. Umbilicus closed or open, very narrow. Dimensions. Height 21–31 mm; width 12–21 mm; ratio height/width 1.5–2.3; number of whorls 5 3/8–6 1/2, height aperture 9–13 mm; width aperture 7–10 mm.

Distribution in Sabah. Rare in W: Crocker range, Trus Madi range, Sinobang; Labuan (old record). Elevation range: 300–1100 m. Primary and secondary forest on limestone bedrock. Also in Sarawak (E part). Endemic to Borneo.

Group 2

Amphidromus martensi O Boettger, 1894

(fig. 107d–e, 110g–k, 117b, map 22c)

Boettger 1894: 66; Fulton 1896: 71; Pilsbry 1900: 158; Von Martens 1908: 262; Haas 1951: 626; Zilch 1953b: 137; Laidlaw & Solem 1961: 554; Solem 1964: 38; Saul 1967: 109; Vermeulen 1996b: 286; Schilthuizen & Rutjes 2001: 421; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2761;

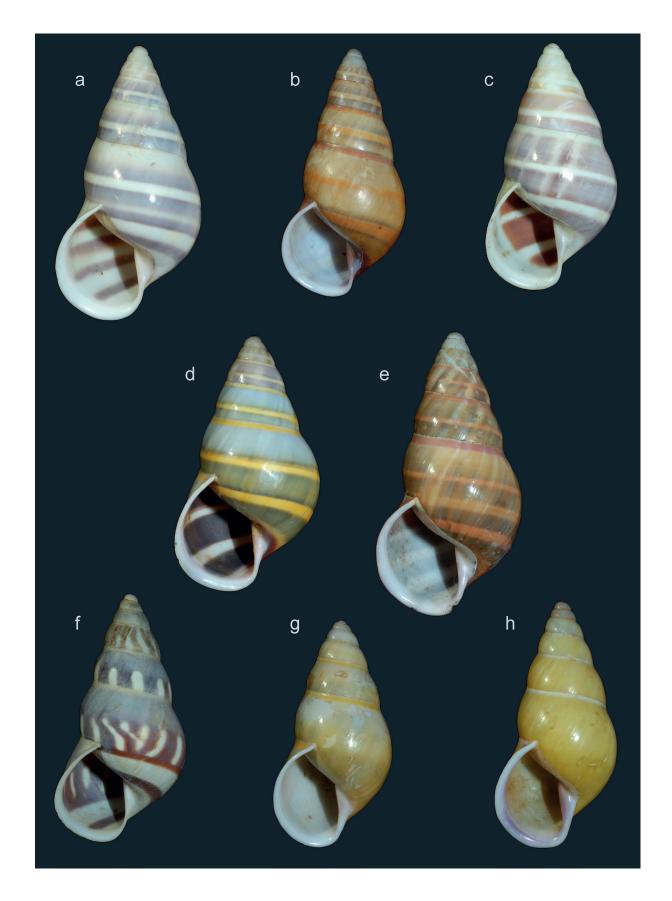


Fig. 109, a–e. *Amphidromus adamsii adamsii* (Reeve, 1848), frontal views, a. Shell 38.5 mm high, b. Shell 35.5 mm high; c. Shell 32 mm high, d. Shell 33 mm high, e. Shell 38.5 mm high; f–h. *Amphidromus adamsii pictus* (Fulton, 1896), frontal views, f. Shell 35.5 mm high, g. Shell 33 mm high, h. Shell 37 mm high.

Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54. – Type from Malaysia, Sabah, mount Kinabalu.

Cross diagnosis. Among Sabah Amphidromus characterized by the wide, ovoid or ellipsoid shell.

Description. Shell sinistral or dextral, large, rather thin, white to lemon yellow to green to reddish brown or reddish purple, usually with a white subsutural band, with or without (pale) blue-purple to brown, somewhat vaguely outlined spiral bands which in some shells are so wide that they cover most of the shell surface, with 2–3 such bands on the last whorl, and 1–2 on the penultimate, apex not darker than the rest of the shell. Spire ovoid or ellipsoid with narrowly rounded apex. Surface shiny. Whorls: First whorls moderately convex, others slightly convex, last whorl evenly rounded. Sculpture. Protoconch approx. smooth at 40x magnification. Teleoconch. Radial sculpture: inconspicuous growth lines, slightly raised at uneven intervals. Spiral sculpture: Some rather fine, shallow, unevenly spaced striation on the first whorls, other whorls locally with traces of very fine striation, just visible at 40x magnification. Aperture inside with approx. the same colors as outside, peristome white, rather thin to rather thick on the parietal side, elsewhere thickened, spreading. Umbilicus closed. Dimensions. Height 29.7–49 mm; width 19.2–32 mm; ratio height/width 1.5–2.0; number of whorls 5–6 7/8, height aperture 16.2–25 mm; width aperture 11.5–22 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary and secondary forest, in coastal vegetation on various types of bedrock. Also in Kalimantan (E part). Endemic to Borneo.

Variability. 1. A form from islands of volcanic origin off Semporna has small shells which are more variable in the ration height/width than mainland specimens. Two shells (out of a sample of 7) also have a small denticle on the parietal side of the aperture, rather deep inside the shell. A similar, smaller denticle occurs in a single mainland shell from the Kinabatangan river valley (sample JV 9632).

2. Specimens from Pun Batu, W of Sapulut, have relatively slender shells, with an aperture with a narrowly rounded basal corner. In the first character they resemble *Amphidromus psephos*, but they are larger.

Amphidromus psephos Vermeulen, Liew & Schilthuizen, 2015

(fig. 107f, 110f, map 22b)

Vermeulen et al. 2015: 59. - Type from Malaysia, Sabah, Interior Prov., Pun Batu c. 30 km W of Sapulut.

Cross diagnosis. Differs from Amphidromus martensi by its smaller and narrower shell.

Description. Shell sinistral, rather large, rather thin, white with or without some inconspicuous, oblique, pale brownish-purple markings; apex not darker than the rest of the shell. Spire elongated-conical with convex sides to approx. narrowly ovoid, apex narrowly rounded. Surface shiny. Whorls: Top whorls convex, other whorls moderately convex but slightly concave just below the suture, last whorl rounded at the periphery. Sculpture. Protoconch minutely rugulose and shallowly punctate. Teleoconch. Radial sculpture: Inconspicuous growth lines, slightly raised at uneven intervals. Spiral sculpture: Locally traces of very fine, shallow striation on the upper whorls only, just visible at 40x magnification. Aperture inside white, peristome thin on the parietal side, elsewhere thickened, spreading. Umbilicus closed or open, very narrow. Dimensions. Height 23.5–25.0 mm; width 10.8–12 mm; ratio height/width 2.1–2.3; number of whorls 5–5 1/2; height aperture 9.0–11.9 mm; width aperture 6.5–8.0 mm.

Distribution in Sabah. Pun Batu only. Elevation range: 500–600 m. Found in shrubby forest on limestone bedrock. Endemic to Sabah.

Genus *Bradybaena* H Beck, 1837

Diagnosis for the Sabah species. Shell dextral, depressed-conical, medium-sized, last whorl (narrowly) rounded, slightly descending towards the aperture or not, its periphery at approx. half-way its height. Apex narrowly rounded. Spiral sculpture present. Periostracum deciduous, greenish, shiny, translucent; periostracal hair-scars on shell surface absent. Aperture at an angle of 45° with the coiling axis or less, not drawn-out into a beak on the palatal side. Umbilicus open, 7–10 % of the shell width. Second whorl 2.2–2.8 mm diameter.

Bradybaena similaris (Férussac, 1822)

(fig. 111a-b, 117c, map 22d)

Rensch 1933a: 200; Van Benthem Jutting 1950: 501; 1959: 166; Saul 1967: 109; Zilch 1968: 185; Vermeulen 1996b: 286; Cowie 1997: 17; Maassen 1997: 84; Vermeulen & Whitten 1998: 128, 158; Maassen 2001: 123; Mordan et al. 2003: (5); Schilthuizen 2004: 95; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 5; Tan et al. 2012: 121; Uchida et al. 2013: 53, 54; Phung et al. 2017: 79; Marzuki et al. 2021: 67. – *Helix similaris* Férussac 1822 (1821–1822): Limaçons 43; Reeve 1851 (1851–1854): Pl. 34, fig. 149; Von Martens 1867: 270. – *Helix (Camaena) similaris* (Férussac) Pfeiffer 1855b: 138. – *Eulota similaris* Pilsbry 1895 (1893–1895): 205. – Type from Indonesia, Timor.

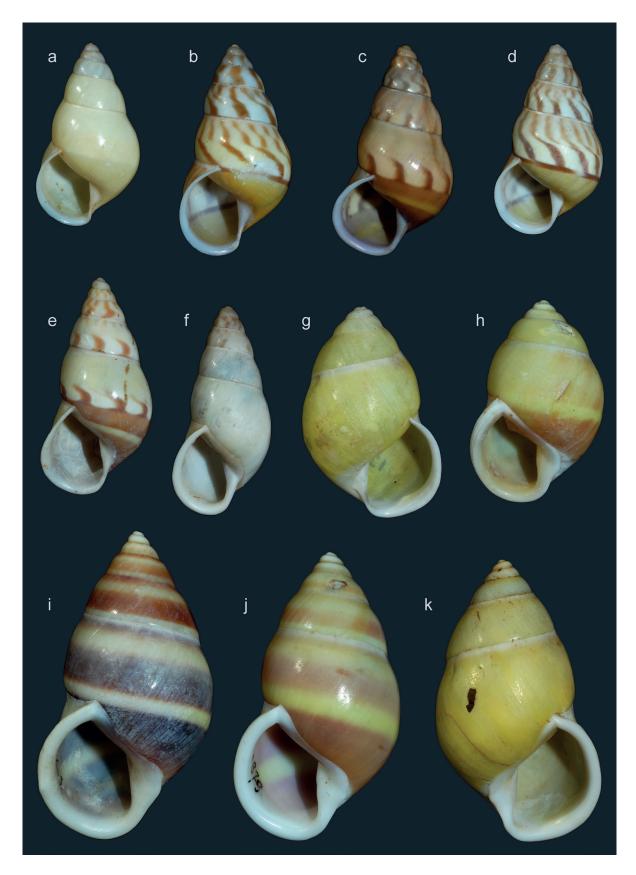


Fig. 110, a–e. *Amphidromus hamatus* Fulton, 1896, frontal views, a. Shell 26.5 mm high, b. Shell 27.5 mm high, c. Shell 29.5 mm high, d. Shell 26.5 mm high, e. Shell 28 mm high; f. *Amphidromus psephos* Vermeulen, Liew & Schilthuizen, 2015, frontal view, shell 24 mm high; g–k. *Amphidromus martensi* O Boettger, 1894, frontal views, g. Shell 32 mm high, h. Shell 31 mm high, i. Shell 46 mm high, j. Shell 44.5 mm high, k. Shell 43 mm high.

Description. Shell dextral, medium-sized, thin, white to pale green-corneous, with or without a thin (pale) brown peripheral band. Spire depressed-conical with a narrowly rounded apex. Surface shiny. Whorls convex, last whorl convex above and below the periphery, periphery rounded to somewhat obtusely angular. Sculpture. Protoconch approx. smooth at 40x magnification. Teleoconch. Radial sculpture: Growth lines, close together, distinctly raised at somewhat uneven intervals, some almost like radial ribs. Spiral sculpture: Locally with subordinate, inconspicuous, shallow, rather densely placed spiral grooves, some more distinct than others; below the periphery, and particularly towards the umbilicus, this striation may be more distinct. Aperture broadly crescent-shaped, columellar side rounded. Peristome not thickened, slightly spreading on the palatal and the basal side, spreading on the columellar side. Umbilicus open. Dimensions. Height 7.9–11.4 mm; width 10.4–15.6 mm; ratio height/ width 0.67–0.82; diameters of the first 2 whorls 1.0–1.3 mm, 2.2–2.8 mm respectively; umbilicus up to 0.7–1.4 mm wide, which is 7–10 % of the shell width; number of whorls 4 3/4–5 1/8; height aperture 5.3–8.0 mm; width aperture 6.2–8.8 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–2200 m. In secondary woodland, agricultural land, gardens, urban areas. Introduced. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: Circumtropical. Natural range: Possibly E Asia.

Variability. Extralimital material shows extensive variability in shell shape and coloration; see Mordan et al. (2003) for pictures. On Borneo, we so far have only encountered shells resembling the form depicted here; the description includes such shells only.

Note. This invasive species was only recently recorded for the first time from Borneo in Uchida et al. (2013); it was never listed by 19th century authors. Perhaps it arrived on Borneo only recently.

Genus *Chloraea* Albers, 1850

Diagnosis for the Sabah species. Shell dextral, depressed-globose, large, last whorl narrowly rounded to obtusely angular, not or hardly descending towards the aperture, its periphery above half-way its height. Apex broadly rounded. Spiral sculpture inconspicuous. Periostracum deciduous, greenish, shiny, translucent, periostracal hairscars on shell surface absent. Aperture at an angle of 45° with the coiling axis or less, not drawn-out into a beak on the palatal side. Umbilicus closed. Diameter second whorl 9.6–10.3 mm.

Notes. 1. Resembles *Chloritis* and *Trachia*, differs by the absence of periostracal hair-scars on the shell surface, and by the wider apical whorls (diameter of the second whorl 9.6–10.3 mm, versus 3.8–7.0 mm).

2. The genus is widespread and speciose in the Philippines and the E part of Indonesia, with a single species crossing the border on an offshore island of Sabah

Chloraea puella (Broderip, 1841)

(fig. 111c-e, 117d, map 22e)

Helix (Caracolla) puella Broderip 1841: 45. – Helix puella (Broderip) Reeve 1851 (1851–1854): Pl. 21, fig. 66. – Helix (Corasia) puella (Broderip) Pfeiffer 1855b: 144. – Cochlostyla puella (Broderip) Semper 1874 (1870–1885): 167. – Corasia puella (Broderip) Pilsbry 1891 (1891–1892): 120. – Helicostyla (Corasia) puella (Broderip) Pilsbry 1895 (1893–1895): 220. – Type from Philippines, island 'Camiguing'.

Helix aegrotus Reeve 1851 (1851–54): Pl. 22, fig. 95. – Helix (Corasia) aegrota (Reeve) Pfeiffer 1855b: 144; Pfeiffer & Clessin 1881: 200. – Corasia aegrota (Broderip) Pilsbry 1891 (1891–1892): 124. – Cochlostyla aegrota Smith 1894c: 54. – Helicostyla (Corasia) aegrota (Reeve) Pilsbry 1895 (1893–1895): 219. – Type from Philippines, Mindoro.

Cochlostyla sp. 'Sabah & S Philippines' Schilthuizen et al. 2013: Online supplementary data.

Description. Shell dextral, large, thin, white, with a thin orange-brown to dark brown peripheral band. Surface shiny. Spire depressed globose with a broadly rounded apex. Whorls: Apical whorls almost flat to slightly convex; other whorls slightly convex above the periphery, often attached just below the periphery of the previous whorl, exposing the distinctly but obtusely angular periphery of the top whorls, last whorl narrowly rounded to obtusely angular at the periphery, slightly to moderately convex below. Sculpture. Protoconch approx. smooth, with a few growth lines. Teleoconch. Radial sculpture: Growth lines, rather close together, with some raised at uneven intervals. Spiral sculpture: Rather inconspicuous, shallow, rather widely and unevenly spaced spiral grooves, some more distinct than others, cutting through the radial sculpture in the first whorls; on the last whorl and below the periphery these are (almost) absent in some shells. Aperture obtusely trapezium-shaped, columellar side straight or slightly sinuous. Peristome not thickened, slightly spreading on the palatal and the basal side, sharply folded and spreading on the columellar side. Umbilicus closed. Dimensions. Height 17.5–18.5 mm; width 26–27 mm; ratio height/width 0.67–0.69; diameters of the first 2 whorls 3.6–4.2 mm, 9.6–10.3 mm respectively; number of whorls 3 3/8–3 5/8, height aperture 12–14 mm; width aperture 15–16 mm.

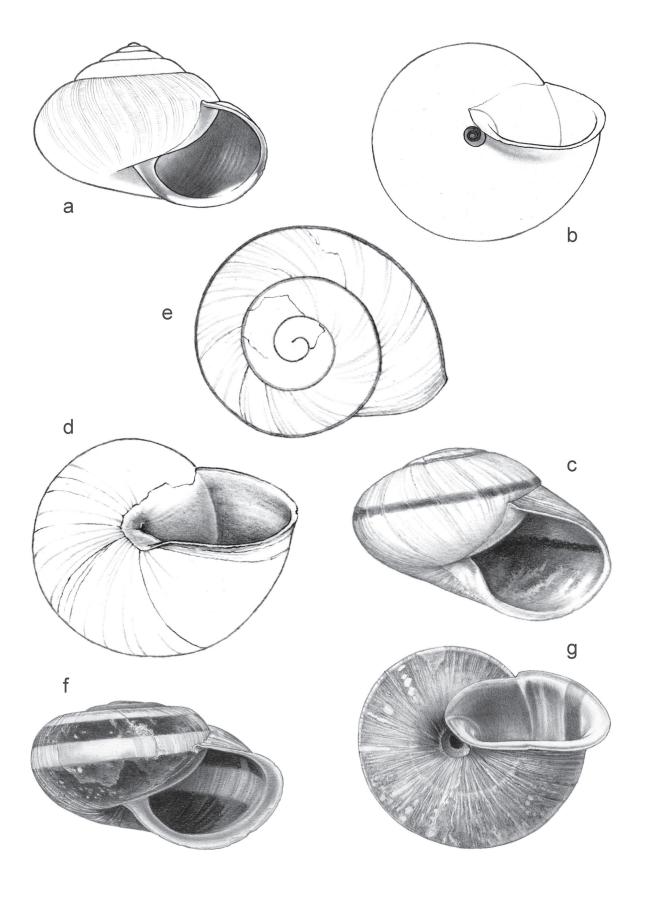


Fig. 111, a–b. *Bradybaena similaris* (Férussac, 1822), a. Frontal view, shell 10 mm high, b. Umbilical view; c–e. *Chloraea puella* (Broderip, 1841), c. Frontal view, shell 18 mm high, d. Umbilical view, e. Apical view; f–g. *Chloritis dulcissima* (E A Smith, 1898), f. Frontal view, shell 10 mm high, g. Umbilical view.

Distribution in Sabah. Tun Sakaran Marine Park only. Elevation range: 0–400 m. Vegetation on volcanic bedrock. Distribution elsewhere: Philippines, Indonesia (Talaud Archipelago).

Note. The Sabah shells are smaller than material from elsewhere, but agree with specimens from Sibutu island, just across the border; see Smith (1894c: 54).

Genus *Chloritis* H Beck, 1837

Diagnosis for the Sabah species. Shell dextral, depressed globose or lenticular, medium-sized, last whorl rounded, slightly descending towards the aperture or not, its periphery at approx. half-way its height or slightly above. Apex rather broadly rounded. Spiral sculpture absent. Periostracum thin, deciduous, shiny, translucent; periostracal hair-scars on shell surface present. Aperture at an angle of 45° with the coiling axis or less, not drawn-out on the palatal side. Umbilicus open, 7–16 % of the shell width.

Chloritis dulcissima (E A Smith, 1898)

(fig. 111f-g, map 22f)

Vermeulen 1996b: 287. – *Planispira dulcissima* Smith 1898b: 33; Von Martens 1908: 262. – Type from Malaysia, Sabah, mount Kinabalu.

Cross diagnosis. Uniquely identified among Sabah *Chloritis* by the distinct coloration. Also, the radial sculpture is more distinct than in the other species, particularly on the upper surface.

Description. Shell dextral, medium-sized, thin, opaque, white but with predominant dark brown banding: One red-brown to dark purple-brown band just above the periphery, above this 1–2 red-brown bands leaving narrow strips of white in between, below this, after a wide strip of white, the red-brown base of the shell. Surface rather dull. Spire slightly raised, with slightly convex sides; apex rounded. Whorls convex; last whorl evenly rounded but slightly shouldered towards the suture and somewhat narrowly rounded around the umbilical impression; last half-whorl with its periphery approx. half-way its height. Sculpture. Radial sculpture: Fine, densely placed and slightly unevenly spaced growth lines, somewhat raised to riblets. No spiral sculpture. Periostracal hair-scars widely spaced or inconspicuous. Aperture obliquely semi-elliptic, somewhat narrowly rounded on the palatal side, widely rounded above and below, basal and columellar side rounded; peristome white, slightly spreading towards the suture, more distinctly so elsewhere. Umbilicus open, not or hardly covered by the extended peristome. Dimensions: Height 10–11 mm; width 16.5–17.5 mm; ratio height/width 0.57–0.65; diameters of the first three whorls 2.5–3.2 mm, 5.5–7.0 mm, 10.5–12 mm respectively; umbilicus 1.5–1.8 mm wide, or 9–11 % of the shell width; number of whorls 3 3/4–4; height aperture 6.0–7.5 mm; width aperture 9.5–10.5 mm. Periostracum rather thick, deciduous, corneous, with short widely spaced hairs, usually extant wherever the periostracum itself is extant.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 1400–1500 m. Forest on sandstone/shale and serpentinite bedrock. Endemic to Sabah.

Note. We assume that this is not a highly colored form of another Sabah *Chloritis* because its shape does not agree with any of these, and because it has more conspicuous sculpture.

Chloritis plena (Godwin-Austen, 1891)

(fig. 112a–b, map 23a)

Smith 1896: 97; Clements et al. 2008: 2761. – *Helix (Chloritis) plena* Godwin-Austen 1891: 44. – *Chloritis (Trichochloritis) plena* (Godwin-Austen) Pilsbry 1893 (1892–1893): 276; 1894 (1893–1895): 124; Von Martens 1908: 262. – Type from Malaysia, Sabah, Labuan island.

Cross diagnosis. Identified among Sabah *Chloritis* by the periphery of the last whorl which is (somewhat) above half-way its height (but see note below *C. suluana*). In this character, it approaches Sabah species of *Trachia* in shape; these differ by the slightly sigmoid palatal peristome, above the periphery.

Description. Shell dextral, medium-sized, thin, opaque or slightly translucent, white to corneous to very pale ochre-brown, usually with a (rather sharply delineated,) narrow, (slightly) darker brown band slightly above the periphery. Surface rather shiny. Spire slightly raised, with straight or slightly convex sides; apex (broadly) rounded. Whorls: First whorls convex, next whorls moderately convex; last whorl narrowly rounded at the periphery, almost flat or slightly convex immediately above and often slightly shouldered below the suture, below the periphery moderately rounded, more narrowly rounded round the umbilical impression; last half-whorl with its periphery slightly above half-way its height. Sculpture. Radial sculpture inconspicuous, rather densely placed to moderately and unevenly spaced growth lines, locally somewhat raised. No spiral sculpture. A very fine, dense granulose-rugulose sculpture just visible at 40x magnification. Periostracal hair-scars densely placed on the whorls around the apex and in the umbilicus, widely spaced elsewhere. Aperture obliquely semi-elliptic, somewhat narrowly rounded on the palatal side, widely rounded above and below, basal and columellar side rounded; peristome white,

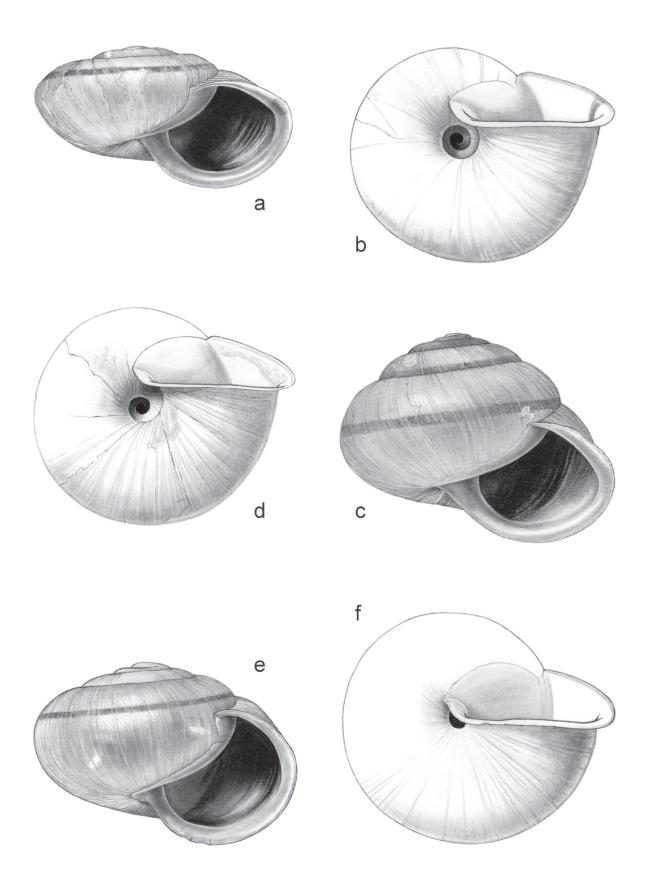


Fig. 112, a–b. *Chloritis plena* (Godwin-Austen, 1891), a. Frontal view, shell 8.5 mm high, b. Umbilical view; c–d. *Chloritis suluana* Von Möllendorff, 1894, c. Frontal view, shell 19 mm high, d. Umbilical view; e–f. *Chloritis tomentosa* (Reeve, 1854), e. Frontal view, shell 9.8 mm high, f. Umbilical view.

slightly spreading towards the suture, more distinctly so elsewhere. Umbilicus open, not covered by the extended peristome. Dimensions: Height 8.0–12.0 mm; width 13.0–20.0 mm; ratio height/width 0.54–0.63; diameters of the first three whorls 2.2–2.5 mm, 4.6–5.5 mm, 8.5–10.5 mm respectively; umbilicus 2.0–2.9 mm wide, or 7.8–11 % of the shell width; number of whorls 3 1/2–4 1/2; height aperture 5.8–9.5 mm; width aperture 7.8–11.0 mm. Periostracum thin, deciduous, pale brown, with short hairs, often extant in the umbilicus only.

Distribution in Sabah. Sapulut only; Labuan (old record). Elevation range: 0–600 m. Primary and secondary forest, with a preference for limestone bedrock. Also in Sarawak. Distribution elsewhere: Indonesia (Sulawesi, a variety).

Chloritis suluana Von Möllendorff, 1894

(fig. 112c-d, 117e, map 23a)

Von Möllendorff 1894: 209. – Type from Philippines, Sulu island.

Helix (? Chloritis) kinibalensis Kobelt 1894 (1880–1897): 706. – Helix (Chloritis) kinibalensis (Kobelt) Smith 1895: 113 ('kinabaluensis'). – Chloritis (Trichochloritis) kinibalensis (Kobelt) Gude 1906: 117 ('kinabaluensis'); Von Martens 1908: 262; Solem 1964: 35. – Chloritis kinibalensis (Kobelt) Saul 1967: 109 ('kinabaluensis'); Vermeulen 1996b: 287 ('kinabaluensis'); Clements et al. 2008: 2761; Schilthuizen & Vermeulen 2003a: 96 ('kinabaluensis'); Schilthuizen et al. 2003b: 41, 42 ('kinabaluensis'); Schilthuizen et al. 2013: Online supplementary data. – Type from Malaysia, Sabah, mount Kinabalu.

Chloritis tomentosa var. major Pfeiffer 1868: 353. – Chloritis tomentosa (not Pfeiffer) Von Martens 1867: 275, partly (specimens a and b). – Type from Malaysia, Sabah, Labuan island.

Chloritis tomentosa auct. Issel 1874: 406.

(?) Xestina belangeri auct. Saul 1967: 110.

Chloritis sibutuensis auct. Clements et al. 2008: 2761; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 95.

[Not Chloritis tomentosa (L Pfeiffer)].

[Not Ariophanta belangeri (Deshayes)].

[Not *Chloritis sibutuensis* (E A Smith)].

Cross diagnosis. Differs from *Chloritis tomentosa* by having a higher spire; forms with a comparatively low spire differ by the profile of the last half-whorl, which is somewhat more narrowly rounded at the periphery than above and below it. Also, *C. suluana* is generally larger.

Description. Shell dextral, medium-sized to rather large, thin, slightly translucent or opaque, (pale) yellow-brown to ochre-brown, with or without a (rather sharply delineated,) (rather) narrow, darker brown band slightly above the periphery. Surface rather shiny. Spire moderately raised to low-conical, with slightly convex sides; apex rounded. Whorls convex; last whorl evenly rounded from suture to the umbilicus, or slightly narrower rounded around the periphery; last half-whorl with its periphery approx. half-way its height. Sculpture. Radial sculpture inconspicuous, densely placed and unevenly spaced growth lines, usually somewhat raised. No spiral sculpture. A very fine, dense granulose-rugulose sculpture just visible at 40x magnification. Periostracal hair-scars densely placed on the whorls around the apex and in the umbilicus, widely spaced or inconspicuous elsewhere. Aperture semi-circular to obliquely semi-elliptic, rounded on the palatal side, usually slightly more widely rounded above and below; peristome white, only slightly spreading towards the suture, distinctly so elsewhere. Umbilicus open, not or hardly covered by the extended peristome. Dimensions: Height 11–28 mm; width 16–33 mm; ratio height/width 0.60–0.92; diameters of the first three whorls 2.4–3.0 mm, 4.8–6.2 mm, 9.0–10.5 mm respectively; umbilicus 2.0–4.5 mm wide, or 9–16 % of the shell width; number of whorls 4 1/2–5 3/4; height aperture 7.0–16.0 mm; width aperture 10.0–19.6 mm. Periostracum very thin, deciduous, pale corneous, with very short (visible at 40x magnification) hairs, usually extant in the umbilicus only.

Distribution in Sabah. Widespread, common. Elevation range: 0–1700 m. Primary and secondary forest, coastal woodland. Distribution elsewhere: Philippines (Sulu archipelago).

Variability. 1. Shells from islands along the N and E coast are often smaller than mainland material.

2. Populations on the Crocker range (samples BOR/MOL 4243, JV 1086) and some shells from Semporna islands have the profile of the last whorl approaching *Chloritis plena*, with its periphery slightly above half-way its height. We include these in *C. suluana* because of the rather high spire (ratio height/width c. 0.7), but they may eventually prove to be a different species.

Chloritis tomentosa (Reeve, 1854)

(fig. 112e–f, map 22f)

Van Benthem Jutting 1959: 163; Marzuki et al. 2021: 68. – *Helix tomentosa* Reeve 1854 (1851–1854): Pl. 199, fig. 1403; Pfeiffer 1855 (1854b): 289; 1859: 271; Von Martens 1867: 275; Pfeiffer 1868: 353; Issel 1874: 406.

Helix (Hygromia) tomentosa (Reeve) Pfeiffer & Clessin 1881: 119. – Helix (Aegista) tomentosa (Reeve) Godwin-Austen 1891: 42. – Chloritis (Trichochloritis) tomentosa (Reeve) Pilsbry 1894 (1893–1895): 124; Von Martens 1908: 262; Solem 1964: 36. – Helix (Chloritis) tomentosa (Reeve) Smith 1895: 100, 113. – Type from Malaysia, Sarawak.

[Not Chloritis tomentosa auct. Issel 1874: 406; = Chloritis suluana Von Möllendorff].

Description. Shell dextral, medium-sized, thin, slightly translucent or opaque, white to pale ochre-brown, with or without a (rather sharply delineated,) (rather) narrow, darker brown band slightly above the periphery. Surface rather shiny. Spire slightly raised, with straight sides; apex rounded. Whorls convex; last whorl rounded at the periphery, slightly less so above and below, slightly shouldered below the suture, narrowly rounded around the umbilical impression; last half-whorl with its periphery approx. half-way its height. Sculpture. Radial sculpture: inconspicuous, rather densely placed and unevenly spaced growth lines, locally somewhat raised. No spiral sculpture. A very fine, dense granulose-rugulose sculpture just visible at 40x magnification. Periostracal hair-scars densely placed on the whorls around the apex and in the umbilicus, rather dense elsewhere. Aperture obliquely semi-elliptic, rounded on the palatal side, slightly more widely rounded above and below, basal side somewhat narrowly rounded, columellar side widely rounded; peristome white, moderately spreading towards the suture, distinctly so elsewhere. Umbilicus open, half-covered by the extended peristome or not. Dimensions: Height 9.2–11.5 mm; width 14.5–17.0 mm; ratio height/width 0.63–0.69; diameters of the first three whorls 2.2–2.8 mm, 4.2–5.0 mm, 8.0–9.7 mm respectively; umbilicus 1.2–2.0 mm wide, or 7–12 % of the shell width; number of whorls 4–4 1/2; height aperture 7.0–8.5 mm; width aperture 8.2–10.0 mm. Periostracum rather thin, deciduous, pale brown, with short hairs, often extant in the umbilicus only.

Distribution in Sabah. Rare in W: Trus Madi range, mount Lumaku, Pun Batu, Sinobang; Banggi island (old record). Elevation range: 300–1100 m. Primary and secondary forest, with a preference for limestone bedrock. Also in Sarawak, Kalimantan. Probably endemic to Borneo (erroneously recorded from Sumatra).

Genus Cochlostyla Férussac, 1821

Diagnosis for the Sabah species. Shell dextral, ovoid-(conical), large, last whorl rounded to obtusely angular, not or hardly descending towards the aperture, its periphery at approx. half-way its height. Apex (rather narrowly) rounded. Spiral sculpture present or absent. Periostracum present, deciduous, greyish brown, dull, opaque, seemingly somewhat fibrous; periostracal hair-scars on shell surface absent. Aperture at an angle of 45° with the coiling axis or less, not drawn-out into a beak on the palatal side. Umbilicus closed. Diameter of second whorl 6.0–8.8 mm.

Note. The genus is widespread and speciose in the Philippines, with only two species crossing the border on small offshore islands of Sabah.

Cochlostyla satyrus (Broderip, 1841)

(fig. 113a-c, 114a, map 23b)

Smith 1893a: 350; Dohrn 1889: 91; Pilsbry 1892 (1892–1893): 13. – *Helix satyrus* Broderip 1841 (1840): 181. – *Bulimus satyrus* (Broderip) Pfeiffer 1848b: 13. – *Bulimus (Amphidromus) satyrus* (Broderip) Pfeiffer 1855b: 146. – *Cochlostyla (Canistrum) satyrus* (Broderip) Pfeiffer & Clessin 1881: 211. – Type from Philippines, Tablas island.

Cochlostyla satyrus (Broderip) var. minima Pilsbry 1892 (1892–1893): 14; Von Martens 1908: 262. – Type of unknown origin.

Cochlostyla satyrus (Broderip) var. cyanocephala Pilsbry 1892 (1892–1893): 14. – Type from 'Borneo; Palawan'.

Description. Shell dextral, large, rather thin, off-white to grey-brown, often with slightly darker streaks approx. following the growth lines. Spire elongated-conical with slightly convex sides, apex rather narrowly rounded. Surface moderately shiny. Whorls: Apical whorls distinctly convex, other whorls slightly convex; last whorl somewhat narrowly rounded to obtusely angular at the periphery. Sculpture. Protoconch seemingly smooth, but slightly and minutely rugose, just visible at 40x magnification. Teleoconch. Radial sculpture: Growth lines, with some raised at uneven intervals. Spiral sculpture: A very fine, dense striation. Aperture white inside, elliptic with the parietal and columellar side truncated, columellar side slightly sinuous. Peristome white, with a purple-brown outer edge, slightly thickened, spreading. Umbilicus closed. Dimensions. Height 42–53 mm; width 23–26.5 mm; ratio height/width 1.79–2.10; diameters of the first 2 whorls 3.2–3.5 mm, 6.5–7.8 mm respectively; number of whorls 5 5/8–6 1/2, height aperture 19–23 mm; width aperture 14.5–16.5 mm. Periostracum little persistent, pale ochre-grey, wearing off along the growth lines or in a zig-zag pattern.

Distribution in Sabah. Islands off Semporna only. Elevation range: 0-100 m. Coastal vegetation on limestone

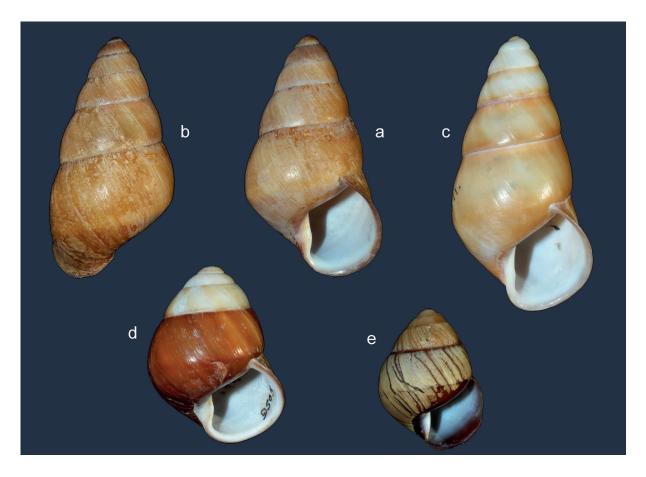


Fig. 113, a—c. *Cochlostyla satyrus* (Broderip, 1841), a. Frontal view, shell 43 mm high b. Back view, c. Frontal view, shell 48 mm high; d—e. *Cochlostyla trailli* (L Pfeiffer, 1855), d. Frontal view, shell 31 mm high, e. Frontal view of subadult shell covered with periostracum, shell 33 mm high.

bedrock. Distribution elsewhere: Philippines.

Notes. 1. Identification as *Cochlostyla satyrus* needs confirmation. Extralimital material of the species has a wider, more rounded apex, and more convex sides of the spire, and more convex whorls; see Pilsbry (1891b: 13). Often, they are also of a darker color.

2. The description includes Sabah material only.

Cochlostyla trailli (L Pfeiffer, 1855)

(fig. 113d-e, 114b, 117f, map 23b)

Issel 1874: 409 ('Cochlostila'); Tenison Woods 1888: 1044; Clements et al. 2008: 2761; Schilthuizen et al. 2011: 5; Foon et al. 2018: 95. – Bulimus trailli Pfeiffer 1855a: 106. – Bulimus (Amphidromus) trailli (L Pfeiffer) Pfeiffer 1855b: 146. – Cochlostyla (Orthostylus) trailli (L Pfeiffer) Pfeiffer & Clessin 1881: 209. – Type from 'Palawan Passage, near Borneo'.

Bulimus cinerosus Pfeiffer 1855a: 107. – Cochlostyla cinerosa (L Pfeiffer) Issel 1874: 410 ('Cochlostila'); Pilsbry 1892 (1892–1893): 15. – Type from 'Palawan Passage, near Borneo'.

Cochlostyla graellsi Hidalgo 1886: 155; Pilsbry 1892 (1892–93): 14. – Type from Philippines, Balabac island.

Cross diagnosis. Shorter, relatively wider and with fewer whorls than *Cochlostyla satyrus* (ratio height/width 1.39–1.64, versus 1.79–2.10).

Description. Shell dextral, large, rather thin to rather thick, first whorls white to pale brown, later whorls increasingly suffused red-brown or orange-brown, often in streaks approx. following the growth lines; last whorl often with a narrow yellow or white band below the suture. Entirely white shells occasionally occur. Surface shiny. Spire elongated-conical with distinctly convex sides, almost ovoid; apex rounded. Whorls: Apical whorls convex, other whorls slightly convex; last whorl somewhat narrowly rounded at the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Growth lines, with some raised at uneven intervals. Spiral sculpture: Local-

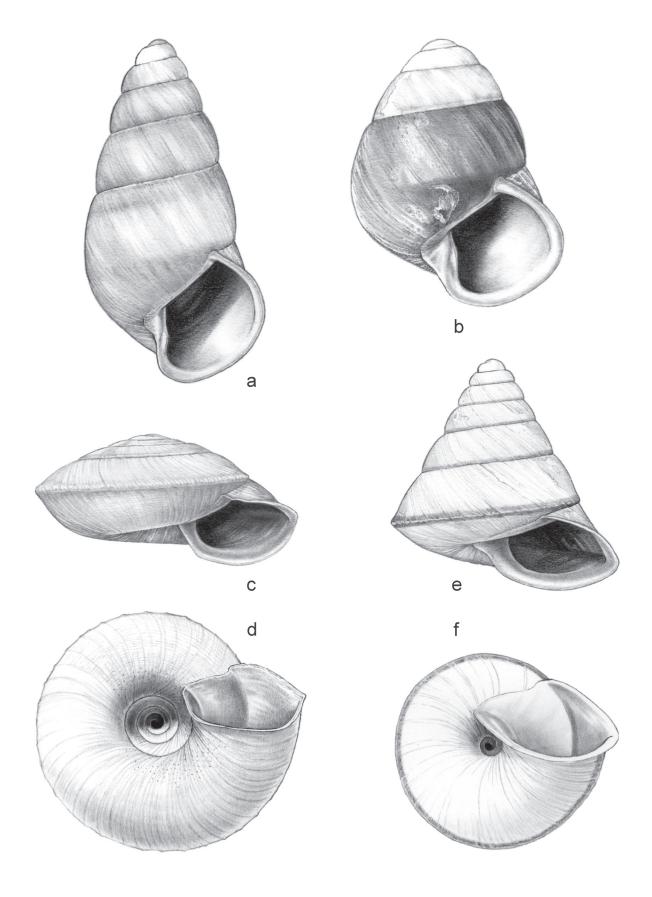


Fig. 114, a. *Cochlostyla satyrus* (Broderip, 1841), Frontal view, shell 50 mm high; b. *Cochlostyla trailli* (L Pfeiffer, 1855), Frontal view, shell 33 mm high; c–d. *Landouria squamulifera* (Von Möllendorff, 1887), c. Frontal view, shell 6 mm high, d. Umbilical view; e–f. *Ganesella acris* (Benson, 1859), e. Frontal view, shell 12 mm high, f. Umbilical view.

ly traces of a faint, very fine, dense striation on the first whorls, absent on the last. Aperture white inside, elliptic with the parietal and columellar side truncated, columellar side slightly sinuous. Peristome white, usually with a purple-brown or red-brown outer edge, slightly thickened, spreading. Umbilicus closed. Dimensions. Height 29–37 mm; width 20–24 mm; ratio height/width 1.39–1.64; diameters of the first 2 whorls 2.6–4.0 mm, 6.0–8.8 mm respectively; number of whorls 4 3/4–5 3/8, height aperture 15.5–19.5 mm; width aperture 13.0–15.5 mm. Periostracum pale ochre-grey.

Distribution in Sabah. Balambangan island only. Elevation range: 0–100 m. Coastal woodland and forest on limestone bedrock. Distribution elsewhere: Philippines (Balabac, Palawan).

Genus Ganesella W T Blanford, 1863

Diagnosis for the Sabah species. Shell dextral, conical, (rather) small, last whorl acutely keeled, slightly descending towards the aperture or not, its periphery at approx. half-way its height. Apex narrowly rounded. Spiral sculpture present, inconspicuous. Periostracum absent or very thin, deciduous, shiny, translucent; periostracal hair-scars on shell surface present. Aperture at an angle of 45° with the coiling axis or less, not drawn-out on the palatal side. Umbilicus open, 3–8 % of the shell width.

Ganesella acris (Benson, 1859)

(fig. 114e–f, map 23c)

Pilsbry 1895 (1893–1895): 170; Gude 1914: 194; Van Benthem Jutting 1959: 160; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 95; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 54; Marzuki et al. 2021: 70. – Helix acris Benson 1859: 387. – Trochomorpha (Nigritella) acris (Benson) Pfeiffer & Clessin 1881: 81. – Type from India, Assam, Khasi Hills.

Geotrochus perakensis Crosse 1879: 199. – Ganesella perakensis (Crosse) Pilsbry 1894 (1893–1895): 170; Maassen 2001: 119. – Type from Malaysia, Perak.

Helix (Geotrochus) bantamensis Smith 1887a: 132; 1887b: 219. – Ganesella bantamensis (E A Smith) Pilsbry 1895 (1893–1895): 170; Van Benthem Jutting 1950: 459. – Type from Indonesia, Java.

Helix (Geotrochus) tigaensis Godwin-Austen 1891: 44. – Helix (Satsuma) tigaensis (Godwin-Austen) Pilsbry 1891 (1891–1892): 85. – Ganesella tigaensis (Benson) Pilsbry 1895 (1893–1895): 170; Phung et al. 2017: 71. – Papuina tigaensis (Godwin-Austen) Van Benthem Jutting 1933: 70. – Type from Malaysia, Sabah, Tiga island

Helix (Geotrochus) subflava Godwin-Austen 1891: 45. – Type from 'Borneo'.

Description. Shell dextral, (rather) small, thin, opaque or slightly translucent, white to pale corneous, with or without a vaguely outlined, thin, ochre-brown peripheral band. Surface dull or somewhat shiny. Spire elongated-conical with straight to slightly concave sides; apex rounded. Whorls: First whorls moderately convex, next whorls slightly convex; last whorl acutely keeled at the periphery, flat to slightly convex above, slightly convex below, more narrowly rounded towards the umbilical impression. Sculpture. Radial sculpture rather distinct, rather densely placed, unevenly spaced growth lines, some of these, at uneven intervals, raised to low, rounded riblets. Spiral sculpture inconspicuous and often only locally present, very fine, densely placed, wavy, very shallow grooves. Periostracal hair-scars fine, inconspicuous, rather widely spaced, densely placed in the umbilical region. Aperture obtusely quadrangular, rounded on the basal side; peristome white, slightly spreading on the palatal side, distinctly so on the basal and columellar side. Umbilicus open, partly covered by the extended peristome or not. Dimensions: Height 8.8–11.5 mm; width 9.0–11.2 mm; ratio height/width 0.92–1.10; diameters of the first three whorls 1.2–1.5 mm, 2.0–2.7 mm, 3.0–3.8 mm respectively; umbilicus 0.3–1.0 mm wide, or 3–8 % of the shell width; number of whorls 5 3/4–6 1/2; height aperture 3.0–4.0 mm; width aperture 5.0–6.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1200 m. Primary and secondary forest, dry coastal forest, plantations. On limestone bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: India (E part), China, Indochina, Malaysia (Peninsula), Indonesia (Sumatra, Java).

Note. Helix tigaensis Godwin-Austen, 1891, has a relatively wide shell but falls within the accepted variability of the species.

Genus Landouria Godwin-Austen, 1918

Diagnosis for the Sabah species. Shell dextral, lenticular, medium-sized, last whorl acutely keeled, slightly descending towards the aperture or not, its periphery slightly above half-way its height. Apex rather broadly round-

ed. Spiral sculpture present. Periostracum thin, shiny, translucent; periostracal hair-scars on shell surface present. Aperture at an angle of 45° with the coiling axis or less, not drawn-out on the palatal side. Umbilicus open, 26–30% of the shell width.

Landouria squamulifera (Von Möllendorff, 1887)

(fig. 114c-d, 117g, map 23d)

Helix (Plectotropis) squamulifera Von Möllendorff 1887b: 290; Tryon 1888 (1888–1889) 59. – Plectotropis squamulifera (Von Möllendorff) Von Möllendorff 1894: 209. – Aegista (Plectotropis) squamulifera (Von Möllendorff) Zilch 1968: 171. – Type from Philippines, Bongao island.

Landouria c.f. winteriana auct. Saul 1967: 109.

[Not Landouria winteriana Pfeiffer].

Description. Shell dextral, medium-sized, thin, opaque or slightly translucent, white to brown-corneous. Surface somewhat shiny. Spire slightly raised to low-conical with convex sides; apex rounded. Whorls: First whorls moderately convex, next whorls slightly to moderately convex; last whorl obtusely to acutely keeled at the periphery, slightly to moderately convex above, moderately convex below, narrowly rounded towards the umbilical impression. Sculpture. Radial sculpture rather distinct, rather densely placed, unevenly spaced growth lines, some of these, at uneven intervals, raised to low, rounded riblets which are most distinct above the periphery, protrude a little from the peripheral keel and continue below the periphery, there almost subordinate to the spiral sculpture. Spiral sculpture fine, densely placed, slightly wavy, very shallow grooves. Periostracal hair-scars visible in the umbilical area only, fine, densely placed. Aperture obtusely 5-angular, rounded on the basal side; peristome white, slightly spreading on the palatal side, distinctly so on the basal and columellar side. Umbilicus open, not covered by the extended peristome. Dimensions: Height 5.0–6.4 mm; width 10.5–13.3 mm; ratio height/width 0.44–0.51; diameters of the first three whorls 1.1–1.4 mm, 2.5–2.9 mm, 4.8–5.1 mm respectively; umbilicus 2.8–4.0 mm wide, or 26–30 % of the shell width; number of whorls 4 1/2–5; height aperture 2.8–4.4 mm; width aperture 4.8–6.0 mm.

Distribution in Sabah. Widespread but rare: Crocker range, Sapulut, Batu Tengar, Semporna. Elevation range: 100–700 m. In (dry) primary and secondary lowland forest, coastal forest. On limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Genus *Obba* H Beck, 1837

Diagnosis for the Sabah species. Shell dextral, depressed conical or lenticular, (rather) large, last whorl rounded or acutely keeled, distinctly descending towards the aperture, its periphery at approx. half-way its height. Apex broadly rounded. Spiral sculpture absent. Periostracum absent or very thin, deciduous, shiny, translucent; periostracal hair-scars on shell surface absent. Aperture at an angle of more than 60° with the coiling axis, slightly drawn-out on the palatal side or not. Umbilicus open, 3–11 % of the shell width.

Obba marginata (O F Müller, 1774)

(fig. 115a-b, 117h, map 23e)

Pilsbry 1894 (1893–1895): 109; Bartsch 1918: 60; Rensch 1933b: 105; Zilch 1964: 251; Schilthuizen et al. 2013: Online supplementary data. – *Helix marginata* Müller 1774: 41; Reeve 1851 (1851–1854): Pl. 30, fig. 129; Smith 1894c: 54. – *Helix (Obba) marginata* (O F Müller) Pfeiffer 1855b: 137; Pfeiffer & Clessin 1881: 180. – *Obbina marginata* (O F Müller) Von Möllendorff 1894: 209; Kobelt 1905 (1905–1916): 5. – Type from Philippines.

Description. Shell dextral, rather large, thin, opaque, white or pale grey-brown, with or without a vague, rather narrow, brown band immediately above and below the periphery, with another, narrower, darker brown band on the upper surface, approx. half-way the width of the whorl and a similar band on the lower surface. Surface dull or slightly shiny. Spire slightly raised with slightly convex sides; apex widely rounded. Whorls: First whorls convex, other whorls slightly convex but slightly concave towards the periphery, periphery acutely keeled; below the periphery slightly convex but around the umbilical impression narrowly rounded; last half-whorl with its periphery approx. half-way its height. Sculpture. Radial sculpture rather distinct, rather densely placed and unevenly spaced growth lines, some distinctly raised. No spiral sculpture. On the upper and lower surface towards the periphery a very fine, dense granulose-rugulose sculpture just visible at 40x magnification, caused by two sets of grooves approx. perpendicular to each other and each at an angle of approx. 45° to the radial sculpture. Aperture narrowly crescent-shaped if the shell is observed frontally (obtusely 5-angled if the aperture is observed frontally, with the basal side evenly rounded); peristome white, somewhat thickened and distinctly spreading. Umbilicus open, not covered by the extended peristome. Dimensions: Height 9.0–9.2 mm; width 21.0–22.5 mm; ratio height/width 0.41–0.43; diameters of the first three whorls 3.5–4.4 mm, 8.0–10.0 mm, 15.0–17.0 mm respectively; umbilicus

2.0–2.5 mm wide, or c. 11 % of the shell width; number of whorls 3 1/2–3 3/4; height aperture if the shell is observed frontally 2.0–3.0 mm (if the aperture is observed frontally 7.0–7.5 mm high); width aperture 11.0–11.8 mm. Periostracum very thin, deciduous, pale corneous.

Distribution in Sabah. Tun Sakaran Marine Park only. Elevation range: 0–300 m. Coastal vegetation. Distribution elsewhere: Philippines (widespread), Indonesia (Sulawesi, Maluku).

Variability. Consists of numerous localized forms, see Bartsch (1918), Rensch (1933b). The Sabah shells agree in shape and coloration with those from nearby Sibutu island, see Smith (1894c). The description includes Sabah material only.

Obba moricandi (L Pfeiffer, 1842)

(fig. 115c-e, map 23e)

Pilsbry 1894 (1893–1895): 108; Zilch 1964: 252. – *Helix moricandi* Pfeiffer 1842: 86; Reeve 1851 (1851–1854): Pl. 15, fig. 58. – *Helix (Obba) moricandi* (L Pfeiffer) Pfeiffer 1855b: 137; Pfeiffer & Clessin 1881: 180. – *Obbina moricandi* (L Pfeiffer) Kobelt 1905 (1905–1916): 26. – Type from Philippines, Bohol.

Cross diagnosis. Differs from Obba marginata by the tooth on the inside of the basal peristome.

Description. Shell dextral, large, thin, opaque, white or cream-colored with a vaguely outlined, narrow, brown band immediately above the periphery and a second below, slightly further down. Surface shiny. Spire somewhat depressed conical with slightly convex sides; apex rounded. Whorls: First whorls convex, other whorls moderately convex, last whorl evenly rounded at the periphery and below. Sculpture. Radial sculpture rather inconspicuous, rather densely placed and unevenly spaced growth lines, some slightly raised. No spiral sculpture. Aperture hardly visible if the shell is observed frontally (ovate if the aperture is observed frontally); peristome white, distinctly thickened and spreading, with a distinct, rounded, slightly inward turned knob approx. half-way along the basal side. Umbilicus open, half-covered by the extended peristome. Dimensions: Height c. 14 mm; width c. 26.5 mm; ratio height/width c. 0.53; diameters of the first three whorls c. 3.5 mm, c. 8.0 mm, c. 14.5 mm respectively; umbilicus c. 0.8 mm wide, or c. 3 % of the shell width; number of whorls c. 4 3/4; height aperture if the shell is observed frontally c. 2.5 mm (if the aperture is observed frontally c. 10 mm); width aperture c. 15 mm. Periostracum very thin, deciduous, pale corneous.

Distribution in Sabah. Malawali island only. Elevation range: 0–100 m. Probably in coastal vegetation. Distribution elsewhere: Philippines.

Genus Trachia Albers, 1860

Diagnosis for the Sabah species. Shell dextral, depressed conical or lenticular, medium-sized, last whorl rounded to obtusely keeled, slightly descending towards the aperture or not, its periphery at approx. half-way its height or distinctly above. Apex broadly rounded. Spiral sculpture absent. Periostracum absent or very thin, deciduous, shiny, translucent (thick in *T. serpentinitica*); periostracal hair-scars on shell surface present. Aperture at an angle of 45° with the coiling axis or less, distinctly drawn-out into a beak on the palatal side or not. Umbilicus closed, or open, up to 19 % of the shell width.

Trachia gabata (Gould, 1843)

(fig. 116a-b, map 23f)

Trachia (Philidora) gabata gabata (Gould) Solem 1964: 32. – Helix (Caracolla) gabata Gould 1843b: 139; 1844: 454; Reeve 1852 (1851–1854): Pl. 127, fig. 766. – Plectotropis gabata (Gould) Wallace 1865: 408. – Helix (Trachia) gabata (Gould) Pfeiffer & Clessin 1881: 181; Tryon 1888 (1888–1889): 57. – Planispira (Trachia) gabata (Gould) Pilsbry 1894 (1893–1895): 116. – Chloritis gabata (Gould) Maassen 2001: 121. – Type from Myanmar, 'Tavoy'.

Cross diagnosis. Differs from *Trachia pudica* by the open, much wider umbilicus (2.2–2.9 mm wide, or 13–19 % of the shell width, versus up to 1 mm wide, or up to 6 % of the shell width). On average, the whorls are more slowly expanding (diameter third whorl 7.5–10.0 mm, versus 9.8–11.3 mm).

Description. Shell dextral, medium-sized, thin, slightly translucent, white or pale yellow-green. Surface rather shiny. Spire only slightly raised with slightly convex sides, apex almost flat or widely rounded. Whorls convex; last whorl obtusely keeled at the periphery, slightly concave immediately above, slightly convex towards the suture, below the periphery moderately convex but around the umbilical impression narrowly rounded; last half-whorl with its periphery distinctly above half-way its height. Sculpture. Radial sculpture inconspicuous, densely placed and unevenly spaced growth lines, usually somewhat raised. No spiral sculpture. A very fine, dense granulose-rugulose sculpture just visible at 40x magnification. Periostracal hair-scars densely placed in the whorls around the apex, widely spaced or inconspicuous elsewhere. Aperture obliquely rhombiform, obtusely angular on the palatal

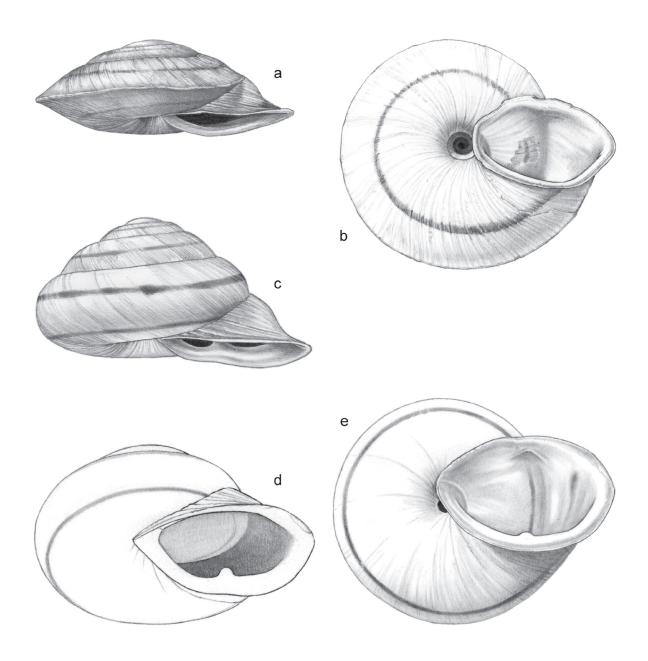


Fig. 115, a–b. *Obba marginata* (O F Müller, 1774), a. Frontal view, shell 7.5 mm high, b. Umbilical view; c–e. *Obba moricandi* (L Pfeiffer, 1842) c. Frontal view, shell 15 mm high, d. Oblique frontal view showing tooth on peristome, e. Umbilical view.

side, approx. straight or slightly concave above, slightly convex below, basal side narrowly rounded, columellar side approx. straight; peristome white, only slightly spreading towards the suture, distinctly so elsewhere. Umbilicus open. Dimensions: Height 7.8–8.8 mm; width 13.0–20.5 mm; ratio height/width 0.43–0.65; diameters of the first three whorls 2.0–2.3 mm, 3.8–4.6 mm, 7.5–10.0 mm respectively; umbilicus 2.2–2.9 mm wide, or 13–19 % of the shell width; number of whorls 3 7/8–4 1/4; height aperture 6.5–7.0 mm; width aperture 9.0–12.0 mm. Periostracum very thin, deciduous, pale corneous, short hairs usually extant in the umbilicus only.

Distribution in Sabah. Widespread but rare: Sapulut, lower Kinabatangan, Tabin. Elevation range: 0–400 m. Primary and secondary lowland forest. Distribution elsewhere: Malaysia (Peninsula), Singapore, Indonesia (Sumatra).

Note. Part of the unresolved *Trachia gabata* species complex, see Rensch (1934b: 331) and Solem (1964: 32). The Sabah shells are not identical with any nominal taxon within the complex, and generally characterized by the slightly more rounded periphery. Within the species complex, most similar are *T. wrayi* (De Morgan, 1885)

(Peninsular Malaysia) which has a slightly wider umbilicus, *T. tanquereyi* (Crosse & P. Fischer, 1863) (Vietnam) which has a more distinctly descending aperture, and *T. fouresi* (Morlet, 1886) (Cambodia) which has a half-covered umbilicus, next to a more distinct peripheral keel. We identify the Sabah shells as *T. gabata* in a wide sense.

Trachia pudica (Godwin-Austen, 1891)

(fig. 116c–d, map 23f)

Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Clements et al. 2008: 2761; Tan et al. 2012: 125; Schilthuizen et al. 2013: Online supplementary data. – *Helix (Aegista) pudica* Godwin-Austen 1891: 43; Pilsbry 1893 (1892–1893): 191. – *Plectotropis pudica* (Godwin-Austen) Von Martens 1908: 262. – *Trachia (Philidora) pudica* (Godwin-Austen) Solem 1964: 33. – Type from Malaysia, Sabah, Labuan island.

Description. Shell dextral, medium-sized, thin, slightly translucent, white or pale yellow-green with a rather sharply delineated, narrow, pale (red-)brown band at the periphery. Surface rather shiny. Spire only slightly raised with slightly convex sides, apex almost flat or widely rounded. Whorls: First whorls convex, next whorls moderately convex; last whorl obtusely keeled at the periphery, slightly concave immediately above and, usually, below, slightly convex towards the suture, further below the periphery slightly convex but around the umbilical impression narrowly rounded and sometimes with almost an obtuse ridge towards the aperture; last half-whorl with its periphery distinctly above half-way its height. Sculpture. Radial sculpture inconspicuous, densely placed and unevenly spaced growth lines, usually somewhat raised. No spiral sculpture. A very fine, dense granulose-rugulose sculpture just visible at 40x magnification. Periostracal hair-scars densely placed on the first whorls around the apex, widely spaced on the lower surface, elsewhere inconspicuous. Aperture obliquely rhombiform, obtusely angular on the palatal side, approx. straight or slightly concave above, slightly convex below, basal side narrowly rounded, columellar side approx. straight; peristome white, only slightly spreading towards the suture, distinctly so elsewhere. Umbilicus closed or open, partly covered by the extended peristome. Dimensions: Height 8.0–9.5 mm; width 17.5-21.0 mm; ratio height/width 0.45-0.51; diameters of the first three whorls 2.2-2.9 mm, 4.8-5.7 mm, 9.8–11.3 mm respectively; umbilicus up to 1 mm wide, or up to 6 % of the shell width; number of whorls 3 7/8–4; height aperture 6.4-7.5 mm; width aperture 10.5-12.5 mm. Periostracum very thin, deciduous, pale corneous, short hairs usually extant in the umbilicus only.

Distribution in Sabah. Danum valley only; Labuan (old record). Elevation range: 0–200 m. Primary and secondary forest. Distribution elsewhere: Malaysia (Peninsula), Singapore, Indonesia (Sumatra).

Species delimitation. Solem (1964: 33) includes *Trachia pudica* in the *Trachia gabata* species complex. In Sabah, we can distinguish two separate forms, one with a (partly) closed, narrow umbilicus, and one with an open, wide umbilicus. We retain the two as species. Further investigation is needed.

Trachia serpentinitica Vermeulen, Liew & Schilthuizen, 2015

(fig. 116e–f, map 23f)

Vermeulen et al. 2015: 61. – Type from Malaysia, Sabah, Sandakan Province, Meliau range N of Telupid, S flank.

Cross diagnosis. Identified among Sabah Camaenidae by its beak-like extension of the palatal side of the aperture. The only Sabah species with a similar beak is *Rhinocochlis nasuta* (Metcalfe, 1852) (Ariophantidae), which has a flat, acutely keeled, entirely white shell without hairs on the periostracum.

Description. Shell dextral, medium-sized, thin, opaque, white with 3 rather narrow, brown bands: One slightly above the periphery, one below the suture and one basal. Surface dull. Spire low-conical with slightly convex sides, apex almost flat. Whorls convex; last whorl rounded below the suture and at the periphery, moderately rounded in between and below the periphery; last half-whorl with its periphery approx. half-way its height. Sculpture. Radial sculpture rather inconspicuous: Growth lines at uneven intervals, locally raised to inconspicuous, rather densely placed, flat riblets. No spiral sculpture. Periostracal hair-scars fine, mainly visible in the umbilical area, granules widely spaced. Aperture obliquely rhombiform, distinctly drawn-out into a narrowly rounded beak on the palatal side, distinctly concave above, approx. straight below, basal side rounded, columellar side approx. straight; peristome white, only slightly spreading above the beak, distinctly so below the beak. Umbilicus closed, covered by the extended peristome. Dimensions: Height c. 11.5 mm; width c. 18.0 mm; ratio height/width c. 0.64; diameters of the first three whorls c. 3.5 mm, c. 7.0 mm, c. 12.0 mm respectively; number of whorls c. 3 7/8; height aperture c. 7.5 mm; width aperture c. 11.5 mm. Periostracum rather thick, easily peeling off in dead shells, translucent, greenish-corneous, with evenly spread, short hairs.

Distribution in Sabah. Meliau range only. Elevation range: 600–700 m. Found in primary forest on serpent-inite bedrock. Endemic to Sabah.

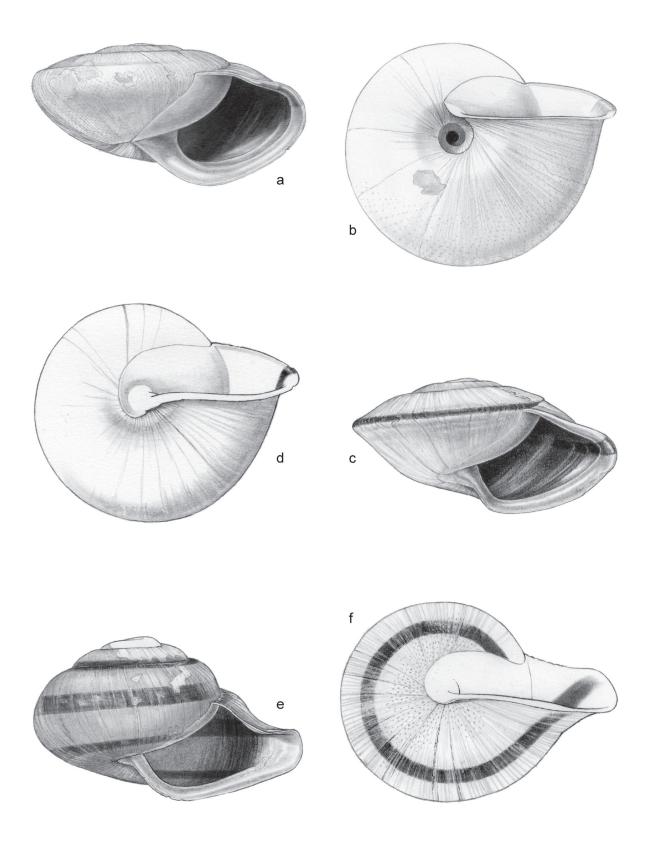


Fig. 116, a–b. *Trachia gabata* (Gould, 1843), a. Frontal view, shell 8.6 mm high, b. Umbilical view; c–d. *Trachia pudica* (Godwin-Austen, 1891), c. Frontal view, shell 9.0 mm high, d. Umbilical view; e–f. *Trachia serpentinitica* Vermeulen, Liew & Schilthuizen, 2015, e. Frontal view, shell 11.5 mm high, f. Umbilical view.

Family **CHAROPIDAE** Hutton, 1884

Diagnosis for the Sabah species. Snails. Shell with up to 3–5 1/4 slowly expanding whorls. Shell dextral, minute, wider than high; discoid with a sunk spire to lenticular with a depressed conical spire; last whorl (narrowly) rounded at or above the periphery. Teleoconch sculpture: Radial sculpture consisting of fine riblets or very distinct, dense ribs (growth lines only in *Leucocharopion*); spiral sculpture very fine, absent in some species. Aperture without teeth (with teeth in *Beilania*). Peristome on the palatal side not thickened, not spreading. Umbilicus closed to open and wide. Dimensions: Adults up to 0.6–1.1 mm high, 1.05–2.2 mm wide.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Either umbilicus closed, or umbilicus open, narrow, less than 10 % of the shell width, and last whorl with a sharp edge inside the umbilical opening

 Genus *Sundacharopa*
- 1 Umbilicus open, wide, 17–46 % of the shell width; last whorl rounded inside the umbilical opening
 - 2 Radial sculpture consisting of a few inconspicuous growth lines only

Genus Leucocharopion

- 2 Radial sculpture consisting of distinct, evenly spaced ribs
 - 3 Spiral sculpture absent on the outer whorls

Genus Discocharopa

- 3 Spiral sculpture present (but fine, subordinate to the coarsest radial sculpture)
 - 4 Microsculpture in between the primary radial ribs consisting of densely placed spiral threads as strong as the secondary radial riblets. Aperture usually with teeth Genus *Beilania*
 - 4 Microsculpture in between the primary radial ribs consisting of well-spaced spiral threads stronger than the secondary radial riblets. Aperture without teeth Genus *Corinomala*

Genus Beilania Preston, 1913

Diagnosis for the Sabah species. Shell brown, opaque, dull. Outline discoid, spire approx. flat or slightly sunk. Radial sculpture consisting of distinct, evenly spaced ribs. Spiral sculpture present. Aperture with teeth. Umbilicus open, wide, 31–36 % of the shell width; last whorl rounded inside the umbilical opening.

Note. Placed in Endodontidae in MolluscaBase (accessed 1/2021). Based on the shell shape, we retain it in Charopidae.

Beilania philippinensis (C G Semper, 1874)

(fig. 118a–b, map 24a)

Solem 1958: 22; Maassen 1997: 57; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 95; Clements et al. 2008: 2761; Marzuki et al. 2021: 76. – Endodonta philippinensis Semper 1874 (1870–1885): 140. – Patula (Endodonta) philippinensis (C G Semper) Pfeiffer & Clessin 1881: 96; Pilsbry 1892 (1892–1893): 82. – Endodonta (Thaumatodon) philippinensis (C G Semper) Pilsbry 1893 (1893–1895): 27. – Type from Philippines, Luzon, Manilla, Antipolo.

Endodonta celebica Sarasin & Sarasin 1899: 175. – Ptychodon celebica (P & F Sarasin) Van Benthem Jutting 1952: 399. – Type from Indonesia, Sulawesi.

Cross diagnosis. Usually characterized among Borneo Charopidae by the teeth in the aperture. Incidental shells of *Beilania philippinensis* without apertural teeth differ from *Corinomala kobelti* by the microsculpture in between the primary radial ribs (densely placed spiral threads as strong as the secondary radial riblets, versus well-spaced spiral threads stronger than the secondary radial riblets).

Description. Shell minute, rather thick, opaque, pale to dark brown. Surface rather dull. Outline discoid, spire approx. flat or slightly sunk. Whorls: Protoconch whorls convex, teleoconch whorls shouldered just below the suture, often slightly flattened above the periphery, last whorl evenly rounded below. Sculpture. Protoconch with rather distinct, rather well-spaced spiral threads. Teleoconch. Radial sculpture: Distinct, rather densely placed, high and narrow radial ribs, in between these very fine (just visible at 40x magnification), densely placed secondary radial riblets. Spiral sculpture: A striation as fine and as densely placed as the secondary radial riblets. Aperture with 1 parietalis; 0–3 palatales, when 1–2 palatales the uppermost absent; aperture rarely without teeth. Umbilicus wide. Dimensions: Height up to 0.9 mm; width up to 2.1 mm; diameter of the first three whorls 0.35–0.45 mm, 0.7–0.9 mm, 1.4–1.65 mm respectively; umbilicus 31–36 % of the shell width; number of whorls up to 3 5/8; height and width aperture up to 0.8 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1200 m. In primary and secondary forest, on limestone and sandstone/shale bedrock. Also in Kalimantan. Distribution elsewhere: Philippines, Indonesia (Sulawesi, Java, Lesser Sunda islands).



Fig. 117, a. Amphidromus hamatus Fulton, 1896; b. Amphidromus martensi O Boettger, 1894; c. Bradybaena similaris (Férussac, 1822); d. Chloraea puella (Broderip, 1841); e. Chloritis suluana Von Möllendorff, 1894; f. Cochlostyla trailli (L Pfeiffer, 1855); g. Landouria squamulifera (Von Möllendorff, 1887), h. Obba marginata (O F Müller, 1774).

Variability. Some specimens lack the apertural teeth; see also note under Corinomala kobelti.

Genus Corinomala Iredale, 1939

(= Pilsbrycharopa Solem, 1958)

Diagnosis for the Sabah species. Shell brown, opaque, dull. Outline discoid, spire not or hardly raised. Radial sculpture consisting of distinct, evenly spaced ribs. Spiral sculpture present. Aperture without teeth. Umbilicus open, wide, 27–28 % of the shell width; last whorl rounded inside the umbilical opening.

Note. Solem (1970) provides an overview of the genus.

Corinomala kobelti (C R Boettger, 1908)

(fig. 118e–f, map 24b)

Charopa kobelti Boettger 1908: 181. – Beilania kobelti (C R Boettger) Van Benthem Jutting 1964: 12. – Pilsbrycharopa kobelti (C R Boettger) Solem 1964: 23; 1970: 243; Clements et al. 2008: 2761; Schilthuizen et al. 2013: Online supplementary data. – Type from Indonesia, Ambon, Cape Tial, Hitu.

Cross diagnosis. Shells of *Beilania philippinensis* without apertural teeth differ by the microsculpture in between the primary radial ribs: Densely placed spiral threads as strong as the secondary radial riblets (well-spaced spiral threads stronger than the secondary radial riblets in *Corinomala kobelti*).

Description. Shell minute, rather thick, opaque, (dark) brown. Surface rather dull. Outline discoid, spire not or hardly raised. Whorls: Protoconch whorls convex, teleoconch whorls shouldered just below the suture, slightly flattened above the periphery, last whorl evenly rounded below. Sculpture. Protoconch with very fine but rather distinct, rather well-spaced, thin spiral threads; with some very fine, subordinate, inconspicuous radial riblets towards the teleoconch. Teleoconch. Radial sculpture: Distinct, rather densely placed, high and narrow radial ribs, in between these very fine (just visible at 40x magnification), densely placed secondary radial riblets. Spiral sculpture: Subordinate to the primary radial ribs but predominant over the secondary riblets; very fine, well-spaced, thin spiral threads. Aperture without teeth. Umbilicus wide. Dimensions: Height up to 1.1 mm; width up to 2.2 mm; diameter of the first three whorls 0.4–0.45 mm, 0.75–0.8 mm, 1. 45–1.6 mm respectively; umbilicus 27–28 % of the shell width; number of whorls up to 3 3/4; height aperture up to 0.8 mm; width aperture up to 0.9 mm.

Distribution in Sabah. Lower Kinabatangan only, an unverified record. Elevation range: 0–100 m. Lowland forest on limestone bedrock. Distribution elsewhere: Indonesia (Ambon, Irian Jaya), Papua New Guinea.

Note. No Sabah material seen by us. The record given above, mentioned by Solem (1964), may be based on a specimen of *Beilania philippinensis* without apertural teeth.

Genus Discocharopa Iredale, 1913

Diagnosis for the Sabah species. Shell white or yellowish, opaque, dull. Outline discoid, spire hardly raised. Radial sculpture consisting of distinct, evenly spaced ribs. Spiral sculpture absent. Aperture without teeth. Umbilicus open, wide, 36–46 % of the shell width; last whorl rounded inside the umbilical opening.

Note. Solem (1983: 76) gives comprehensive information on the genus.

Discocharopa aperta (Von Möllendorff, 1888)

(fig. 118c–d, map 24c)

Solem 1983: 76; 1988: 538; Maassen 1997: 57; Vermeulen & Whitten 1998: 95, 149; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 80; Foon et al. 2018: 95. — Patula aperta Von Möllendorff 1888: 89; Pilsbry 1892 (1892–1893): 80. — Type from Philippines, Luzon, Montalban.

Charopa microdiscus Van Benthem Jutting 1951: 28. – Charopa (Discocharopa) microdiscus (Van Benthem Jutting) Van Benthem Jutting 1952: 398. – Discocharopa microdiscus (Van Benthem Jutting) Solem 1958: 21. – Type from Indonesia, Sulawesi, Macassar, Pankadjene.

Cross diagnosis. Differs from *Beilania* and *Corinomala* by the absence of spiral sculpture. Generally, shells of *Discocharopa* are also of much paler color.

Description. Shell minute, rather thick, opaque, white or yellowish. Surface rather dull. Outline discoid, spire hardly raised. Whorls: Protoconch whorls convex, teleoconch whorls approx. evenly rounded. Sculpture. Protoconch with distinct, high, densely placed radial ribs slightly coarser than on the teleoconch; no spiral sculpture visible at 40x magnification. Teleoconch. Radial sculpture: Distinct, densely placed, high and narrow radial ribs, in between microscopically (barely visible at 40x magnification), densely placed secondary riblets. Spiral sculp-

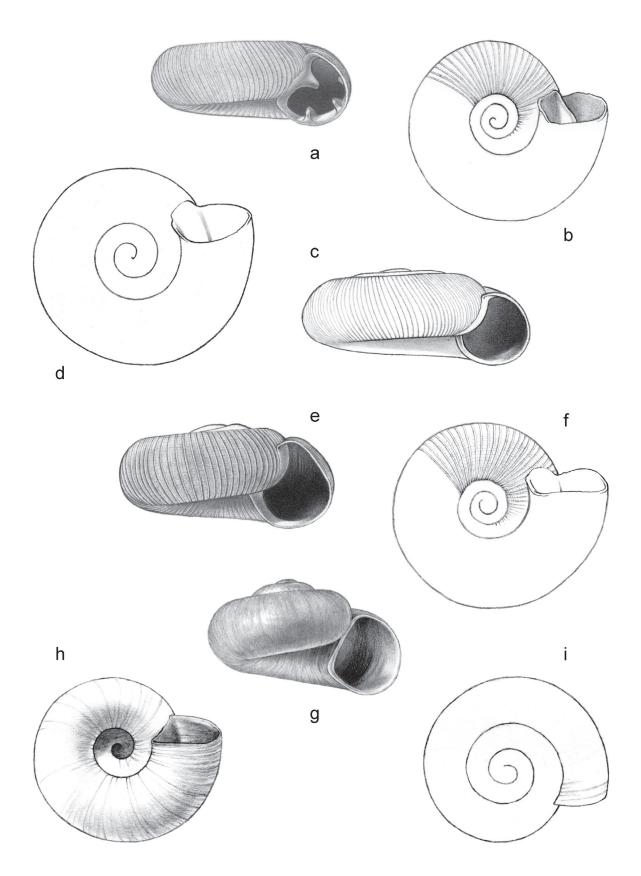


Fig. 118, a–b. *Beilania philippinensis* (C G Semper, 1874), a. Frontal view, shell 0.45 mm high, b. Umbilical view; c–d. *Disco-charopa aperta* (Von Möllendorff, 1888), c. Frontal view, shell 0.5 mm high, d. Umbilical view; e–f. *Corinomala kobelti* (C R Boettger, 1908), e. Frontal view, shell 1.15 mm high, f. Umbilical view.; g–i. *Leucocharopion lissoderma* Vermeulen & Liew, new species, g. Frontal view, shell 0.55 mm high, h. Umbilical view, i. Apical view.

ture not visible at 40x magnification Aperture without teeth. Umbilicus wide. Dimensions: Height up to 0.6 mm; width up to 1.5 mm; diameter of the first three whorls 0.4–0.45 mm, 0.75–0.95 mm, 1.25–1.5 mm respectively; umbilicus 36–46 % of the shell width; number of whorls up to 3 1/2; height aperture up to 0.4 mm; width aperture up to 0.4 mm.

Distribution in Sabah. Scattered localities in W; rather common in E: Ulu Segama and further S; elsewhere Batu Timbang only. Elevation range: 0–800 m. Rainforest, dry forest, secondary forest, coastal vegetation. Also in Kalimantan. Distribution elsewhere: Indonesia to Australia, E-wards to American Samoa.

Genus Leucocharopion Vermeulen & Liew, new genus

Type species: Leucocharopion lissoderma Vermeulen & Liew, new species

Diagnosis for the Sabah species. Shell white or slightly yellowish, translucent, glossy. Spire low-conical, apex narrowly rounded. Radial sculpture consisting of a few inconspicuous growth lines only. Spiral sculpture absent. Aperture without teeth. Umbilicus open, wide, 17–26 % of the shell width; last whorl rounded inside the umbilical opening.

- *Note*. 1. While the species below resembles Bornean *Beilania*, *Corinomala* and *Discocharopa* in general shell shape, it is uniquely identified among Asiatic charopids with a wide umbilicus by its lack of prominent sculpture. We cannot place it, and therefore create a new genus to accommodate it.
- 2. More likely to be an operculate species related to Cyclophoridae according to Páll-Gergely (pers. comm.), because the peristome is attached to the penultimate whorl over a short distance only. We did not find any operculum stuck in otherwise very fresh-looking shells.

Name derivation. From λευκός (Ancient Greek) = white, and the diminutive of the genus name *Charopa*, possibly from $\chi \alpha \rho o \pi o \zeta = bright$, or bluish grey.

Leucocharopion lissoderma Vermeulen & Liew, new species

(fig. 118g-i, map 24d)

Type specimens from Indonesia, Kalimantan Selatan, Meratus mountains, W flank, Nateh near Bata Tangga, c. 18 km E of Barabai (holotype HNHM 104884, paratypes JV 3039/>50 shells).

Macrocycloides sp. 'V2877' Schilthuizen et al. 2011: 5.

Macrocycloides sp. 1 Clements et al. 2008: 2762.

Cross diagnosis. Among Sabah Charopidae characterized by the absence of sculpture, combined with the open, wide umbilicus.

Description. Shell minute, thin, translucent, white or slightly yellowish. Surface glossy. Spire low-conical, apex narrowly rounded. Whorls: Protoconch whorls convex, teleoconch whorls evenly rounded, suture somewhat channeled. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: A few inconspicuous growth lines only. Spiral sculpture absent. Aperture without teeth. Umbilicus wide. Dimensions. Height up to 0.75 mm; width up to 1.05 mm; diameter of the first three whorls 0.27–0.30 mm, 0.57–0.61 mm, 0.95–1.05 mm respectively; umbilicus 17–26 % of the shell width; number of whorls up to 3 1/4; height aperture up to 0.48 mm; width aperture up to 0.45 mm.

Distribution in Sabah. Balambangan island only. Elevation range: 0–100 m. Dry coastal forest; elsewhere in dry secondary forest distant from the coast. Also in Kalimantan (SE part). Endemic to Borneo.

Similar species elsewhere. The general shape of the shell is indicative of Asiatic Charopidae, except for its lack of conspicuous sculpture. In this respect, the shell resembles some New Guinea Rhytididae, such as *Ouagapia microtheca* Van Benthem Jutting, 1964, and *O. occlusa* Van Benthem Jutting, 1964. *Leucocharopion lissoderma* is smaller and lacks sculpture in the umbilicus.

Name derivation. From λισσός (Ancient Greek) = smooth, and δέρμα = skin.

Genus Sundacharopa Vermeulen & Liew, new genus

Type species: Sundacharopa lissobasis Vermeulen & Liew, new species

Diagnosis for the Sabah species. Shell white to yellowish green or brown, opaque to translucent, shiny or with a silky luster. Radial sculpture consisting of growth lines, with or without fine riblets or grooves. Spire hardly raised to low-conical; apex (narrowly) rounded. Spiral sculpture present or absent. Aperture without teeth. Umbilicus closed or open but very narrow, less than 10 % of the shell width and with a sharp edge inside the umbilical opening.

Notes. 1. Van Benthem Jutting (1959) used the generic name Charopa for two minute, densely coiled, finely

sculptured species resembling the seven described below (*C. caloglypta* Van Benthem Jutting, 1959, and *C. perlata* Van Benthem Jutting, 1959, both from Sumatra), although they differ considerably from the generic type, *Charopa coma* (Gray, 1843), from New Zealand. Later, *Microcystina clarkae* Maassen, 2000 was added, a similar species. Together, the ten species represent a Sundaland group of, presumably, Charopidae characterized within the family by their extremely small size, a very narrow or closed umbilicus and the absence of predominant and distinct radial ribs, although a fine and dense sculpture is present. We propose a new genus name for this group. Next to the seven species below, we include:

Sundacharopa caloglypta (Van Benthem Jutting, 1959). – Charopa caloglypta Van Benthem Jutting 1959: 135.

Sundacharopa clarkae (Maassen 2000). – Microcystina clarkae Maassen 2000: 144.

Sundacharopa perlata (Van Benthem Jutting, 1959). – Charopa perlata Van Benthem Jutting 1959: 135.

- 2. The genus *Microcystina* includes similar forms, albeit slightly larger on average, with a finer, usually less distinct sculpture giving the shells a smooth appearance.
 - 3. Check also Punctidae, a family including somewhat similar forms.

Name derivation. Referring to the Sunda shelf, the continental shelf underlying Java, Sumatra, and Borneo, in combination with the genus name *Charopa*, possibly from $\chi \alpha \rho o \pi o \varsigma$ (Ancient Greek) = bright, or bluish grey.

KEY TO THE GROUPS

1 – Umbilicus open in adult shells, shallow. Shell white

- Group 3
- 1 Umbilicus closed, shell rarely rimate. Shell usually pale yellowish green to brown (rarely white in S. lissobasis)
 - 2 Spiral sculpture above the periphery fine but distinct, at most slightly subordinate to the radial sculpture. Shell diameter 0.85–0.95 mm at three whorls

 Group 1
 - 2 Spiral sculpture above the periphery absent or inconspicuous, clearly subordinate to the radial sculpture. Shell diameter 1.0–1.2 mm at three whorls

 Group 2

Group 1

Sundacharopa infrastriata Vermeulen & Liew, new species

(fig. 119a-b, map 24e)

Type specimens from Malaysia, Sabah, Kinabalu N.P., Bundu Tuhan (holotype BOR/MOL 4013); Malaysia, Sabah, upper Padas river valley, sandstone outcrops along tributary of Matang river, S of Long Pasia (paratypes JV 9921/14 shells).

Charopa infrastriata, unavailable name, Clements et al. 2008: 2761–2762.

Charopa sp. 2 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Differs from *Sundacharopa jugalis* by the higher spire and the wider aperture. Also, the spiral grooves are usually more spaced, particularly below the periphery. These differences hold for juvenile as well as adult shells.

Description. Shell minute, rather thin, about opaque, brown. Surface shiny. Spire rather low conical with approx. straight sides; apex narrowly rounded. Whorls: Protoconch whorls convex, first teleoconch whorls convex, last whorl rounded around the periphery, more narrowly rounded and shouldered above, widely rounded below, basis rounded. Sculpture. Protoconch with distinct, densely placed radial riblets coarser than on the teleoconch; traces only of a spiral sculpture consisting of rows of slight depressions, one depression in between each pair of radial riblets. Teleoconch. Radial sculpture: Above the periphery scattered growth lines and locally patches of fine, densely placed, low riblets which all gradually disappear below the periphery. Spiral sculpture: Above the periphery a slightly subordinate striation, consisting of moderately spaced rows of minute pits; below the periphery predominant, fine but distinct, widely spaced grooves over the entire surface. Aperture crescent-shaped. Umbilicus closed. Dimensions: Height up to 0.8 mm; width up to 1.4 mm; diameter of the first three whorls 0.3–0.35 mm, 0.55–0.6 mm, 0.85–0.9 mm respectively; number of whorls up to 4 1/2; height aperture up to 0.6 mm; width aperture up to 0.7 mm.

Distribution in Sabah. Scattered localities in W, common at mount Kinabalu; elsewhere rare: Meliau range and Tawau hills. Elevation range: 100–3000 m. Damp places in primary forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Name derivation. From infra (Latin) = underneath, and striatus = grooved.

Sundacharopa jugalis Vermeulen & Liew, new species

(fig. 119c-d, map 24f)

Type specimens from Malaysia, Sabah, lower Kinabatangan river valley, unnamed limestone hill near Sukau Police Station (holotype BOR/MOL 2178); Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak

(paratypes JV 9793/>50 shells).

Charopa sp. 'BO-02' Schilthuizen et al. 2002: 256, 257; Schilthuizen et al. 2003b: 42; Schilthuizen 2004: 95. Charopa jugalis, unavailable name, Clements et al. 2008: 2761.

Charopa sp. 'jugalis' Phung et al. 2017: 82.

Cross diagnosis. Differs from *Sundacharopa infrastriata* by the lower spire and the narrower aperture. Also, the spiral grooves are usually less spaced, particularly below the periphery. These differences hold for juvenile as well as adult shells.

Description. Shell minute, rather thin, about opaque, brown. Surface with a silky luster. Spire hardly raised to low conical with concave to convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls convex, first teleoconch whorls slightly convex, last whorl rounded around the periphery, narrowly rounded and shouldered above, rounded below the periphery. Sculpture. Protoconch with distinct, densely placed radial riblets; spiral sculpture consisting of 4–5 rows of minute pits, one pit in between each pair of radial riblets; sculpture coarser than on the teleoconch. Teleoconch. Radial sculpture: Above the periphery scattered growth lines and approx. evenly spaced shallow, vaguely outlined grooves, locally patches of very fine (just visible at 40x magnification) densely placed, low riblets; all gradually disappearing below the periphery. Spiral sculpture: Above the periphery a slightly subordinate striation, consisting of rather densely placed rows of minute pits, or cutting into the crests of the radial riblets; below the periphery predominant, fine but distinct, rather densely placed grooves over the entire surface. Aperture rather narrowly crescent-shaped. Umbilicus closed. Dimensions: Height up to 0.9 mm; width up to 1.9 mm; diameter of the first three whorls 0.3–0.4 mm, 0.50–0.65 mm, 0.70–0.95 mm respectively; number of whorls up to 5 1/4; height aperture up to 0.7 mm; width aperture up to 1 mm.

Distribution in Sabah. Scattered localities in S and E; common in lower Kinabatangan, but less common than Sundacharopa lissobasis. Elevation range: 0–1100 m. In primary and secondary forest on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Name derivation. From iugum (Latin) = yoke, referring to the shouldered whorls.

Sundacharopa platycephala Vermeulen & Liew, new species

(fig. 119e–f, map 25a)

Type specimens from Malaysia, Sabah, Kinabalu N.P., Mesilau trail (holotype BOR/MOL 4161; paratype JV 14333/1 shell).

Charopa sp. 5 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Characterized within Group 1 by the flat protoconch whorls. Also, its aperture is narrower than in any other species of this group.

Description. Shell minute, rather thin, about opaque, (pale) brown. Surface rather glossy. Spire low conical with convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls flat, first teleoconch whorls moderately convex, last whorl evenly rounded, only slightly shouldered above the periphery. Sculpture. Protoconch with distinct, low, densely placed radial riblets slightly coarser than on the teleoconch, no spiral sculpture. Teleoconch. Radial sculpture: Above and below the periphery scattered growth lines and approx. evenly spaced, shallow, and vaguely outlined grooves, locally (patches of) much finer, densely placed, sharply outlined grooves in between. Spiral sculpture: Above and below the periphery barely subordinate, fine, continuous, rather well-spaced grooves. Aperture narrowly crescent-shaped. Umbilicus closed. Dimensions: Height up to 0.85 mm; width up to 1.5 mm; diameter of the first three whorls 0.35–0.4 mm, 0.6–0.65 mm, 0.85–0.9 mm respectively; number of whorls up to 4 5/8; height aperture up to 0.7 mm; width aperture up to 1 mm.

Distribution in Sabah. Widespread but rare: Mount Tambuyukon, mount Kinabalu, Sapulut. Elevation range: 500–2200 m. In primary and secondary forest on sandstone/shale bedrock. Endemic to Sabah.

Name derivation. From πλατύς (Ancient Greek) = flat, and κεφαλή = head, referring to the flat protoconch whorls.

Group 2

Sundacharopa lissobasis Vermeulen & Liew, new species

(fig. 120a-b, map 25b)

Type specimens from Malaysia, Sabah, Kiansom Falls near Kota Kinabalu (holotype BOR/MOL 3463); Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (paratypes JV 7504/9 shells).

Charopa sp. 'BO-01' Schilthuizen et al. 2002, 256, 257; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 95.

Charopa 'V9744' Schilthuizen 2004: 95.

Charopa lissobasis, unavailable name, Clements et al. 2008: 2761.

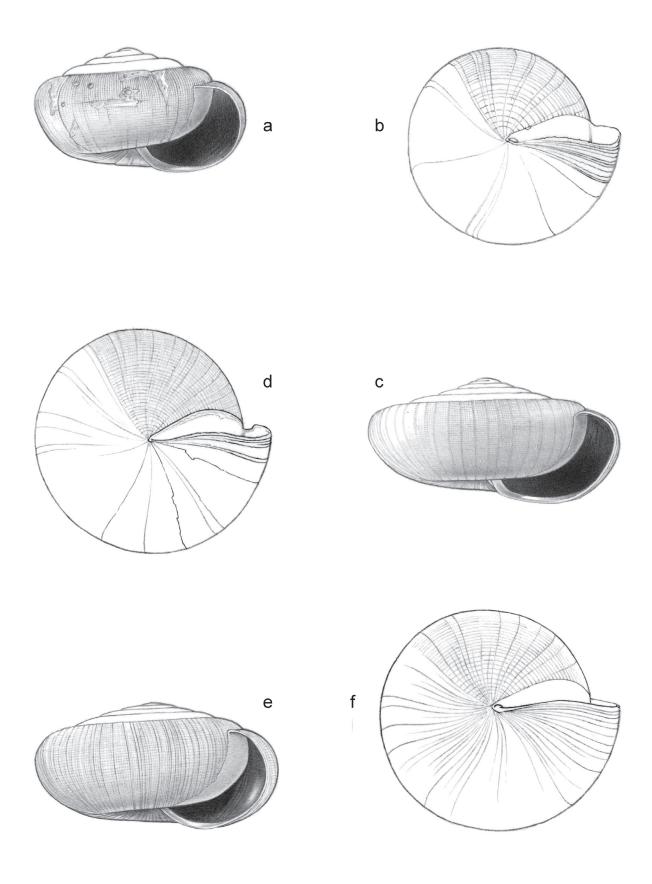


Fig. 119, a–b. *Sundacharopa infrastriata* Vermeulen & Liew, new species, a. Frontal view, shell 0.8 mm high, b. Umbilical view; c–d. *Sundacharopa jugalis* Vermeulen & Liew, new species, c. Frontal view, shell 1.0 mm high, d. Umbilical view; e–f. *Sundacharopa platycephala* Vermeulen & Liew, new species, e. Frontal view, shell 0.85 mm high, f. Umbilical view.

Charopa sp. 3 Liew et al. 2010: Online Supporting Information, Appendix S1. *Charopa* sp. '*lissobasis*' Phung et al. 2017: 82.

Cross diagnosis. Apart from the characters in the key to the groups, this differs from *Sundacharopa jugalis* and *S. infrastriata* by the less distinct spiral sculpture on the lower surface. Often, spiral striation is only present towards the periphery, but sometimes it extends towards the umbilicus. Such shells differ from the species mentioned because the striation is fine (just visible at 40x magnification), inconspicuous and dense, and often only present in patches. The radial ribs above the periphery are usually denser than in *S. jugalis* and *S. infrastriata*.

Description. Shell minute, thin, slightly translucent, brown, rarely white, Surface shiny. Spire moderately low conical with straight to convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls convex, first teleoconch whorls convex, last whorl evenly rounded with only a slight shoulder above the periphery. Sculpture. Protoconch with distinct, densely placed radial riblets slightly coarser than on the teleoconch; with subordinate, approx. continuous, densely placed spiral grooves. Teleoconch. Radial sculpture: Above the periphery very fine, densely placed, low riblets that gradually disappear below the periphery. Spiral sculpture: Above the periphery subordinate to almost absent, densely placed, fine grooves cutting into the crests of the radial riblets only; this spiral sculpture becomes more distinct and predominant around and somewhat below the periphery, but is (almost) absent lower down, towards the umbilicus. Aperture crescent-shaped. Umbilicus closed, rarely rimate. Dimensions: Height up to 1.0 mm; width up to 1.5 mm; diameter of the first three whorls 0.35–0.40 mm, 0.65–0.70 mm, 1.0–1.1 mm respectively; number of whorls up to 4 1/4; height aperture up to 0.55 mm; width aperture up to 0.70 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary and secondary forest on limestone, sandstone, volcanic, and serpentinite bedrock. Endemic to Sabah.

Name derivation. From λισσός (Ancient Greek) = smooth, and βάσις = base.

Sundacharopa turgidula Vermeulen & Liew, new species

(fig. 120c–d, map 25c)

Type specimens from Malaysia, Sabah, Kinabalu N.P., Mesilau area (holotype BOR/MOL 4145). *Charopa* sp. 6 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Differs from *Sundacharopa lissobasis* in having a higher body whorl, combined with a very low spire.

Description. Shell minute, thin, slightly translucent, pale yellowish green. Surface shiny. Spire low conical with straight to convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls convex, first teleoconch whorls moderately convex, last whorl somewhat broadly rounded around and below the periphery, slightly narrowly rounded above and around the basis. Sculpture. Protoconch with distinct, densely placed radial riblets, slightly coarser than on the teleoconch; spiral sculpture absent. Teleoconch. Radial sculpture: Fine, densely placed, low riblets, below the periphery almost as distinct as above. Spiral sculpture above the periphery subordinate to absent, rather well-spaced, fine grooves cutting into the crests of the radial riblets; below the periphery this spiral sculpture becomes slightly coarser but is still present only in patches. Aperture crescent-shaped. Umbilicus closed, rarely rimate. Dimensions: Height up to 1.1 mm; width up to 1.6 mm; diameter of the first three whorls c. 0.5 mm, c. 0.75 mm, c. 1.2 mm respectively; number of whorls up to 4; height and width aperture up to 0.8 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 800–3100 m. In montane and subalpine forest on granodiorite bedrock. Endemic to Sabah.

Name derivation. From the diminutive of turgidus (Latin) = swollen.

Group 3

Note. The transition from protoconch to teleoconch, mentioned in the descriptions below, is visible as an area with a slight concentration of uneven riblets, after the comparatively smooth protoconch.

Sundacharopa argos Vermeulen & Liew, new species

(fig. 120e–f, map 25d)

Type specimens from Malaysia, Sabah, upper Padas river valley, Long Pa Sia (holotype BOR/MOL 4351); ditto, S of Long Pasia, sandstone outcrops along tributary of Matang river, (paratypes JV 9818/6 shells).

Charopa argos, unavailable name, Clements et al. 2008: 2761; Foon et al. 2018: 95.

Charopa sp. 1 Liew et al. 2010: Online Supporting Information, Appendix S1.

Charopa sp. 'argos' Marzuki et al. 2021: 84.

Cross diagnosis. Differs from *Sundacharopa cancellatula* by the more narrowly rounded and slightly shouldered outer whorl above the periphery, as well as by the less prominent or almost absent spiral sculpture, most conspicuously present below the periphery.

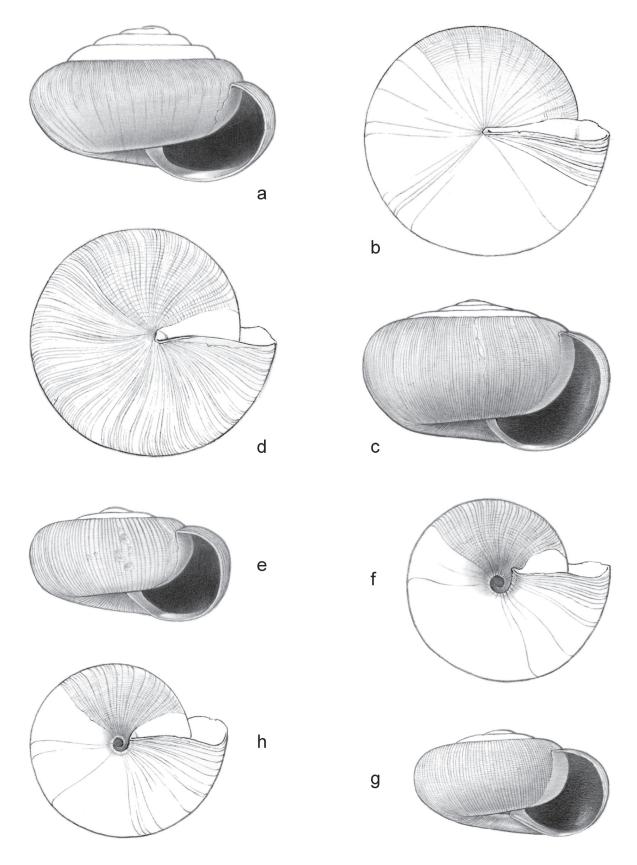


Fig. 120, a–b. *Sundacharopa lissobasis* Vermeulen & Liew, new species, a. Frontal view, shell 0.95 mm high, b. Umbilical view; c–d. *Sundacharopa turgidula* Vermeulen & Liew, new species, c. Frontal view, shell 1.0 mm high, d. Umbilical view; e–f. *Sundacharopa argos* Vermeulen & Liew, new species, e. Frontal view, shell 0.95 mm high, f. Umbilical view; g–h. *Sundacharopa cancellatula* Vermeulen & Liew, new species, g. Frontal view, shell 0.9 mm high, h. Umbilical view.

Description. Shell minute, rather thin, slightly translucent, white. Surface shiny. Spire low conical to hardly raised, with straight to convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls convex, first teleoconch whorls convex, last whorl broadly rounded around and below the periphery, more narrowly rounded and slightly shouldered above, more narrowly rounded at the basis. Sculpture. Protoconch with distinct, fine, densely placed radial riblets slightly coarser than on the teleoconch; spiral sculpture consisting of widely spaced rows of minute pits. Teleoconch. Radial sculpture: Fine, rather widely and unevenly spaced to locally densely placed, shallow, narrow to wide, sharply delineated grooves, below the periphery almost as distinct as above. Spiral sculpture sometimes almost absent, usually present in scattered patches, very fine, densely placed grooves, below the periphery slightly more prominent than above. Aperture somewhat broadly crescent-shaped. Umbilicus closed in juveniles, open in adults but very narrow, somewhat over 1 whorl deep, last whorl with a sharp edge inside the umbilical opening. Dimensions: Height up to 0.6 mm; width up to 1.1 mm; diameter of the first three whorls 0.3–0.35 mm, 0.6–0.7 mm, 1.0–1.1 mm respectively; number of whorls up to 3; protoconch 1/2–5/8 whorl; height aperture up to 0.55 mm; width aperture up to 0.55 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary forest on limestone and sandstone/shale bedrock. Also in Brunei, Sarawak, Kalimantan. Endemic to Borneo.

Name derivation. From ἀργός (Ancient Greek) = shining, glistening.

Sundacharopa cancellatula Vermeulen & Liew, new species

(fig. 120g-h, map 25e)

Type specimens from Malaysia, Sabah, lower Kinabatangan river valley, Mawas hill (holotype BOR/MOL 14836; paratypes JV 13494/32 shells).

Charopa sp. 4 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Differs from *Sundacharopa argos* by the more evenly rounded whorls, as well as by the more prominent spiral sculpture which extends over most of the shell surface.

Description. Shell minute, rather thin, slightly translucent, white. Surface with a silky luster. Spire low conical to hardly raised, with straight to convex sides; apex (narrowly) rounded. Whorls: Protoconch whorls convex, first teleoconch whorls convex, last whorl evenly rounded, slightly shouldered above the periphery. Sculpture. Protoconch with distinct, fine, densely placed radial riblets slightly coarser than on the teleoconch; spiral sculpture consisting of widely spaced rows of minute pits. Teleoconch. Radial sculpture: Fine, (rather) densely and somewhat unevenly placed, shallow, narrow, sharply delineated grooves, below the periphery almost as distinct as above. Spiral sculpture: Very fine, densely placed grooves over the entire surface, below the periphery slightly more prominent than above. Aperture somewhat broadly crescent-shaped. Umbilicus closed in juveniles, open in adults but very narrow, somewhat over 1 whorl deep, last whorl with a sharp edge inside the umbilical opening. Dimensions: Height up to 0.55 mm; width up to 1.15 mm; diameter of the first three whorls c. 0.3 mm, c. 0.6 mm, 0.95–1.15 mm respectively; number of whorls up to 3; protoconch 3/4–7/8 whorl; height aperture up to 0.4 mm; width aperture up to 0.55 mm.

Distribution in Sabah. Widespread but rare: Mount Kinabalu, lower Kinabatangan, Tawau hills. Elevation range: 0–600 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Name derivation. From the diminutive of cancellatus (Latin) = with a criss-cross pattern.

Family **CHRONIDAE** Thiele, 1931

Diagnosis for the Sabah species. Snails. Shell with up to 3 1/8–7 7/8 slowly to rather rapidly expanding whorls. Shell dextral, (very) small, approx. as high as wide or somewhat wider than high; shell almost ovoid to conical to almost lenticular; last whorl rounded to acutely keeled at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth lines, in many species also with fine riblets without a periostracal crest (with very distinct ribs in Rahula), spiral sculpture absent or present, fine; sculpture not prominent (but prominent in Rahula), often giving she shell a silky luster. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed, or open but narrow. Dimensions: Adults up to 1.6–6.0 mm high, 1.8–6.2 mm wide.

Genus Kaliella W T Blanford, 1863

Diagnosis for the Sabah species. Radial sculpture teleoconch prosocline, consisting of fine growth lines or densely placed to moderately spaced fine riblets. Last whorl without prominent spiral threads (numerous very fine spiral threads may be present), or with 1 spiral thread or keel at the periphery.

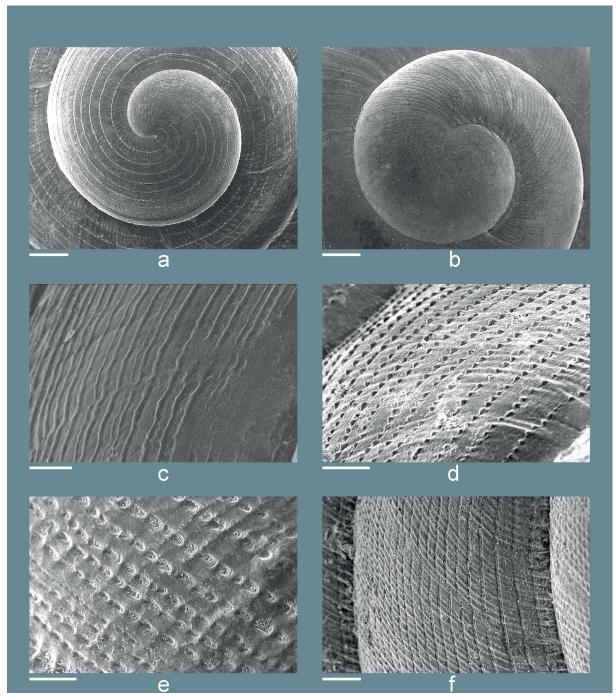


Fig. 121, a. *Kaliella microconus* (Mousson, 1865), apex; b. *Kaliella accepta* (E A Smith, 1895), apex; c. *Kaliella nephelophila* (Tillier & Bouchet, 1989), upper surface of the third whorl; d. *Kaliella dendrophila* (Van Benthem Jutting, 1950), upper surface of the third whorl; e. *Kaliella punctata* Vermeulen, Liew & Schilthuizen, 2015, upper surface of the third whorl; f. *Kaliella calculosa* (Gould, 1852), upper surface of the third whorl. Scale bars: a–b. 0.1 mm; c–f. 0.05 mm.

KEY TO THE GROUPS

- 1 Protoconch with spiral threads clearly predominant over the radial sculpture (fig. 121a)
- Group 1
- 1 Protoconch with spiral threads as strong as the radial sculpture or weaker, or protoconch without spiral sculpture (fig. 121b)
 - $2-Diameter\ of\ the\ third\ whorl\ more\ than\ 2.3\ mm$

Group 2

- 2 Diameter of the third whorl 2.2 mm or less
 - 3 Periphery of last whorl rounded in adult shells (rounded to angular in juveniles), and without peripheral thread **Group 3**
 - 3 Periphery of last whorl angular in adult shells, or with a peripheral spiral thread

4 – Spiral sculpture teleoconch fine but distinct above the periphery

- Group 4
- 4 Spiral sculpture teleoconch absent or inconspicuously present in patches, only just discernible at 40x magnification Group 5

Group 1

Kaliella dendrophila (Van Benthem Jutting, 1950)

(fig. 121d, 122a-b, map 25f)

Liardetia dendrophila Van Benthem Jutting 1950: 407; Van Benthem Jutting 1959: 138; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 84; Foon et al. 2018: 96. – Type from Indonesia, Java.

[Not Kaliella dendrophila auct. Phung et al. 2017: 88; = K. olivacea Vermeulen].

Cross diagnosis. Characterized within Group 1 by the spiral sculpture on the teleoconch, above the periphery, which consists of rows of minute beads. *Kaliella gregaria* and *K. microsoma* have similar shells but a spiral sculpture not consisting of rows of beads.

Description. Shell very small, thin, translucent, very pale greenish to yellowish. Surface shiny. Spire somewhat depressed-conical with straight sides; apex rounded. Whorls: Top whorls convex, outer whorls (almost) flat, last whorl acutely angular at the periphery, almost flat or slightly convex above and below. Sculpture. Protoconch with distinct, moderately spaced, rounded spiral threads, radial sculpture absent or inconspicuous, subordinate. Teleoconch. Radial sculpture: Above the periphery with some rather distinct, unevenly spaced, somewhat raised growth lines, next to these locally some very fine, inconspicuous, moderately spaced, low and thin riblets; below the periphery with a few inconspicuous, unevenly spaced growth lines only. Spiral sculpture: A slight, obtuse keel present around the periphery; above and below with rather distinct, well-spaced (particularly half-way between suture and periphery, as well as just below the periphery) threads, which consist of rows of densely placed beads which are often elongated in the direction of the growth lines. Umbilicus open, very narrow, or closed. Aperture obtusely quadrangular, peristome not widened, not thickened. Dimensions. Height up to 2.7 mm; width up to 4.1 mm; diameters of the first four whorls 0.55–0.67 mm, 1.1–1. 5 mm, 2.1–2.7 mm, c. 3.6 mm respectively; number of whorls up to 4 1/2; height aperture up to 1.6 mm; width aperture up to 2 mm.

Distribution in Sabah. Widespread but generally rare: Banggi island, Crocker range, Batu Timbang, lower Kinabatangan (there rather common). Elevation range: 0–700 m. In primary and secondary forest on limestone bedrock. Distribution elsewhere: Malaysia (Peninsula), Indonesia (Java, Sulawesi, Ambon).

Note. Van Benthem Jutting (1950: 407) describes the spiral striation as engraved into the shell surface. SEM images show that it consists of interrupted spiral threads.

Kaliella humilis (Tillier & Bouchet, 1989)

(fig. 122c–e, map 25f)

Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 81. – *Kionghutania humilis* Tillier & Bouchet 1989 (1988): 275; Vermeulen 1996b: 288. – Type from Malaysia, Sabah, Kinabalu N.P.

Cross diagnosis. In the spiral sculpture, *Kaliella humilis* resembles *K. microconus*, but differs by the wider shell (diameter 4th whorl 2.35–2.50 mm, versus 1.45–2.00 mm) and the more convex, slightly shouldered whorls. Also, it has more numerous and more densely placed spiral threads (approx. 30 on the fifth whorl, versus 15 or fewer). Sympatric *K. kinabaluensis* and *K. nephelophila* differ by the slightly more concave outline of the spire, whorls without a shoulder, by the much finer and less distinct spiral threads above the periphery, and by the virtual absence of spiral sculpture below the periphery.

Description. Shell very small, thin, about opaque, greenish brown. Surface shiny. Spire conical with straight or slightly convex sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, outer whorls moderately convex and somewhat shouldered, last whorl angular at the periphery, slightly convex below the periphery. Sculpture. Protoconch with predominant, very fine, well-spaced, thin spiral threads, radial sculpture inconspicuous. Teleoconch. Radial sculpture: Above the periphery with raised growth lines at uneven intervals, most distinctly so just below the suture; below the periphery the growth lines are less distinct. Spiral sculpture predominant, above the periphery with fine, very densely placed, somewhat unevenly spaced, thin spiral threads (approx. 30 on the fifth whorl); below the periphery with very fine, very widely spaced threads, with or without numerous still finer, densely placed grooves in between. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 3.3 mm; width up to 4.1 mm; diameters of the first four whorls 0.6–0.7 mm, 1.05–1.15 mm, 1.6–1.7 mm, 2.35–2.50 mm respectively; number of whorls up to 5 7/8; height aperture up to 1.4 mm; width aperture up to 2 mm.

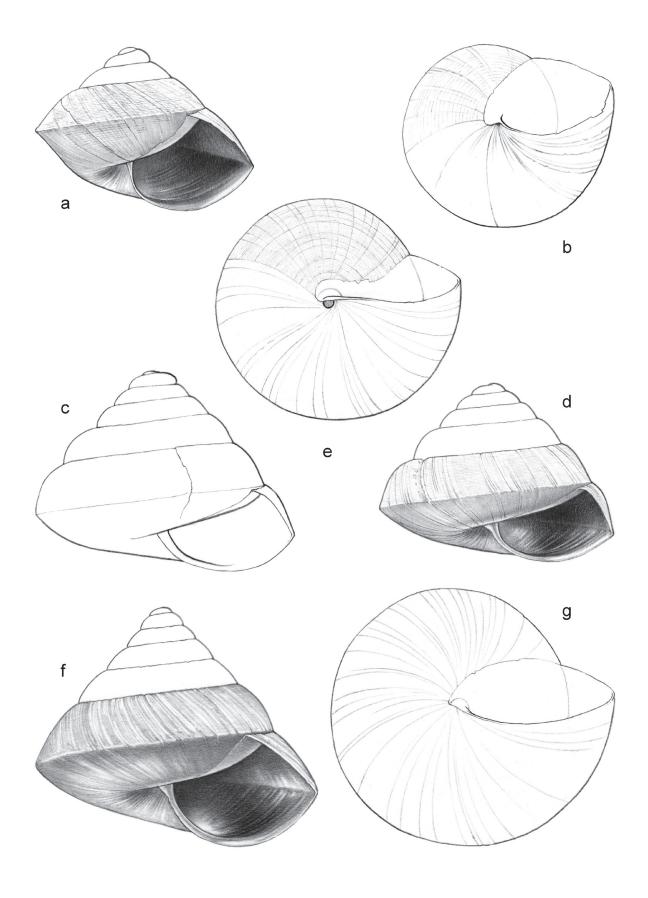


Fig. 122, a–b. *Kaliella dendrophila* (Van Benthem Jutting, 1950), a. Frontal view, shell 2.7 mm high, b. Umbilical view; c–e. *Kaliella humilis* (Tillier & Bouchet, 1989), frontal views, c. Shell 3.3 mm high, d. Shell 2.8 mm high; e. Umbilical view; f–g. *Kaliella kinabaluensis* (Tillier & Bouchet, 1989), f. Frontal view, shell 5.3 mm high, g. Umbilical view.

Radula. Central 3-cuspid; laterals 3-cuspid; marginals serrate with 2 large cones at the tip.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3000–3400 m. In lower montane to subalpine forest on granodiorite and sandstone/shale bedrock. Endemic to Sabah.

Note. However inconspicuous, the spiral sculpture below the periphery is a diagnostic character for *Kaliella humilis*: very fine, widely scattered spiral threads, often with still much finer, very densely placed spiral grooves in between.

Kaliella kinabaluensis (Tillier & Bouchet, 1989)

(fig. 122f–g, map 26a)

Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 84. – *Kionghutania kina-baluensis* Tillier & Bouchet 1989 (1988): 271; Vermeulen 1996b: 288. – Type from Malaysia, Sabah, Kinabalu N.P.

Description. Shell small, very thin, somewhat translucent, slightly greenish brown. Surface shiny. Spire conical with straight or slightly concave sides; apex rounded. Whorls moderately convex and not shouldered, last whorl angular at the periphery, moderately convex below the periphery. Sculpture. Protoconch with spiral sculpture predominant but inconspicuous, very fine, well-spaced, thin threads; radial sculpture inconspicuous. Teleoconch. Radial sculpture: Above the periphery with coarse, distinctly raised growth lines at uneven intervals; below the periphery these are slightly less distinct. Spiral sculpture: Subordinate, on the first whorls with traces of very inconspicuous, moderately-spaced striation, outer whorls above the periphery with a very fine, very densely placed, somewhat wavy striation (more than 100 striae on the fifth whorl); below the periphery almost smooth, with faint traces of an even finer spiral striation only towards the periphery. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus closed. Dimensions. Height up to 5.6 mm; width up to 6.2 mm; diameters of the first four whorls 0.8–0.85 mm, 1.2–1.3 mm, 1.80–1.95 mm, c. 2.7 mm respectively; number of whorls up to 6 1/8; height aperture up to 2.4 mm; width aperture up to 3.2 mm.

Radula. Central 3-cuspid; laterals 3-cuspid; marginals serrate with 2 large cones at the tip.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3000–3400 m. In subalpine forest on granodiorite bedrock. Endemic to Sabah.

Kaliella microconus (Mousson, 1865)

(fig. 121a, 123a-b, 128a, map 26a)

Schilthuizen 2004: 95; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 78; Phung et al. 2017: 89; Marzuki et al. 2021: 73. – Nanina microconus Mousson 1865: 192. – Nanina (Thalassia) microconus (Mousson) Pfeiffer & Clessin 1881: 47. – Coneuplecta (Sitalina) microconus (Mousson) Baker 1941: 236; Solem 1988: 545. – Coneuplecta microconus (Mousson) Van Benthem Jutting 1964: 21; Saul 1967: 109; Maassen 1997: 58; Vermeulen & Whitten 1998: 98, 150; Maassen 2001: 96; Tan et al. 2012: 104. – Liardetia microconus (Mousson) Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2003a: 96; Schilthuizen et al. 2003b: 42. – Type from Fiji.

Sitala bandongensis Boettger 1890: 141. – Coneuplecta bandongensis (O Boettger) Van Benthem Jutting 1950: 388; 1959: 140. – Type from Indonesia, Java, Bandung, mount Malabar.

Sitala baritensis Smith 1893b: 343; 1895: 112; Von Martens 1908: 261. – Durgellina baritensis (E A Smith) Rensch 1932: 68. – Type from Malaysia, Sarawak, 'Barit mountain'.

Sitala singularis Godwin-Austen 1891: 39. - Type from Malaysia, Borneo.

Cross diagnosis. Differs from *Kaliella humilis*, *K. kinabaluensis* and *K. nephelophila* by the more slowly expanding whorls (diameter of the 4th whorl 1.45–2.00 mm, versus 2.35–2.7 mm). It also differs from these species by the coarser and more distinct spiral sculpture (usually 15 or fewer threads above the periphery on the fifth whorl, versus 30 or more).

Description. Shell very small, thin, somewhat translucent, pale brown. Spire conical with straight sides; apex rounded. Surface shiny. Whorls: Top whorls convex, outer whorls slightly convex, last whorl angular at the periphery, slightly convex above and below the periphery. Sculpture. Protoconch with predominant, well-spaced, very thin spiral threads, and very fine, densely placed and somewhat unevenly spaced radial riblets. Teleoconch. Radial sculpture: Above the periphery growth lines grading into very fine, densely placed and somewhat unevenly spaced riblets; below the periphery with unevenly spaced growth lines only. Spiral sculpture predominant, above the periphery fine, well-spaced, very thin threads (usually 15 or fewer on the fifth whorl); below the periphery and close to it with a few to many more of such threads, towards the umbilicus sometimes with much finer, densely placed grooves. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, very narrow. Dimensions. Height up to 3.0 mm; width up to 2.9 mm; diameters of the first four whorls 0.45–0.60 mm, 0.75–1.00 mm, 1.05–1.45 mm, 1.45–2.00 mm respectively; number of whorls up to 6 1/8; height aperture up to 0.9 mm;

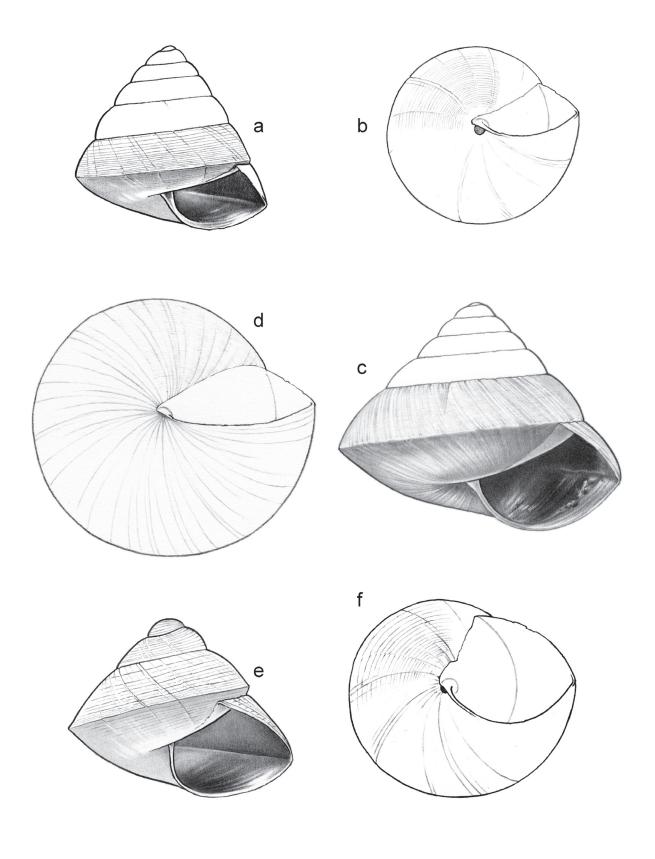


Fig. 123, a–b. *Kaliella microconus* (Mousson, 1865), a. Frontal view, shell 2.3 mm high, b. Umbilical view; c–d. *Kaliella nephelophila* (Tillier & Bouchet, 1989), c. Frontal view, shell 3.5 mm high, d. Umbilical view; e–f. *Kaliella olivacea* (Vermeulen, 1996), e. Frontal view, shell 1.8 mm high, f. Umbilical view.

width aperture up to 1.4 mm.

Radula. central 3-cuspid; laterals and marginals similar, serrate with 2 large cones at the tip.

Distribution in Sabah. Widespread, common. Elevation range: 0–1200 m, elsewhere up to 1700 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Vietnam, Malaysia (Peninsula), Singapore, Indonesia (S-wards to Java), E-wards to Australia, Fiji, Samoa.

Note. Information on the radula is from Van Benthem Jutting (1950). No Sabah material included in *Kaliella microconus* has been checked for radula characters.

Kaliella nephelophila (Tillier & Bouchet, 1989)

(fig. 121c, 123c–d, map 26b)

Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 82. – *Kionghutania nephelophila* Tillier & Bouchet 1989 (1988): 276; Vermeulen 1996b: 288. – Type from Malaysia, Sabah, Kinabalu N.P.

Cross diagnosis. Resembles *Kaliella kinabaluensis*. Diagnostic is the spiral sculpture above the periphery: Fine but still distinct spiral threads, particularly towards the periphery, in *K. nephelophila*; versus an indistinct, dense spiral striation in *K. kinabaluensis*.

Description. Shell very small, very thin, somewhat translucent, slightly brownish green. Surface shiny. Spire conical with straight or slightly concave sides; apex rounded. Whorls: Protoconch whorls rather flat, next whorls slightly to moderately convex and not shouldered, last whorl angular at the periphery, slightly to moderately convex below the periphery. Sculpture. Protoconch with predominant, fine, somewhat inconspicuous, well-spaced, thin spiral threads; radial sculpture inconspicuous. Teleoconch. Radial sculpture: Above the periphery with distinctly raised growth lines at uneven intervals; below the periphery these are slightly less distinct. Spiral sculpture: First whorls with moderately spaced, thin spiral threads, outer whorls above the periphery with fine, rather densely placed, somewhat wavy spiral threads (less than 80 on the fifth whorl) which are slightly more distinct towards the periphery; below the periphery without spiral sculpture, or locally with fine spiral striation. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus almost closed. Dimensions. Height up to 3.8 mm; width up to 4.6 mm; diameters of the first four whorls 0.65–0.80 mm, 1.05–1.20 mm, 1.60–1.75 mm, c. 2.7 mm respectively; number of whorls up to 5 5/8; height aperture up to 1.9 mm; width aperture up to 2.4 mm.

Radula. Central 3-cuspid; laterals 3-cuspid; marginals serrate with 2 large cones at the tip.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3000–3100 m. In upper montane forest on granodiorite bedrock. Endemic to Sabah.

Note. Kaliella kinabaluensis and K. nephelophila differ anatomically; see Tillier and Bouchet (1989).

Kaliella olivacea (Vermeulen, 1996)

(fig. 123e-f, map 26a)

Coneuplecta olivacea Vermeulen 1996c: 155; 1996d: 9. Vermeulen & Whitten 1998: 98, 150; Tan et al. 2012: 103. – Type from Indonesia, Bali.

Kaliella dendrophila auct. Phung et al. 2017: 88.

[Not Kaliella dendrophila Van Benthem Jutting].

Cross diagnosis. Characterized within Group 1 by its small size combined with the rather coarse spiral threads. The latter character also distinguishes it from juvenile shells of other Sabah *Kaliella*.

Description. Shell minute, very thin, transparent, yellow-corneous to green-corneous. Surface shiny. Spire conical with straight sides; apex rounded. Whorls: Apical whorls convex, not shouldered, last whorl acutely angular or slightly keeled at the periphery, almost flat above, slightly convex below. Sculpture. Protoconch with predominant spiral sculpture: Distinct, fine, well-spaced, thin threads; radial sculpture consisting of some crenulation below the suture. Teleoconch. Radial sculpture: Above the periphery with coarse, distinctly raised growth lines at uneven intervals, which are particularly coarse below the suture, and less distinct below the periphery. Spiral sculpture: Predominant, distinct, evenly and well-spaced, thin, sharply delineated threads, on the last whorl the threads in the middle part between suture and periphery with a shallow depression in between with traces of a finer spiral striation, and with an inconspicuous furrow in the deepest point; immediately below the periphery with some finer threads. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, rimate. Dimensions. Height up to 1.8 mm; width up to 2.4 mm; diameters of the first three whorls 0.4–0.7 mm, 0.9–1.3 mm, 1.5–2.2 mm respectively; number of whorls up to 3 1/8; height aperture up to 1.0 mm; width aperture up to 1.3 mm.

Distribution in Sabah. W Coast Islands only. Elevation range: 0–100 m. In coastal vegetation. Distribution elsewhere: Malaysia (Peninsula), Singapore, Indonesia (Bali, Tanimbar islands).

Note. A widespread species, apparently occurring in localized populations, usually in coastal regions. In Peninsular Malaysia it has also been found inland.

Group 2

Check also:

Kaliella punctata (Group 4). Some shells having a third whorl of 2.2 mm diameter; these differ from species in Group 2 by the spiral sculpture which consists of small pits.

Kaliella eurytrochus Vermeulen, Liew & Schilthuizen, 2015

(fig. 124a–c, map 26b)

Vermeulen et al. 2015: 86. - Type from Malaysia, Sabah, Interior Prov., mount Trus Madi slopes, Gua Loloposon.

Cross diagnosis. Differs from *Kaliella gregaria* by its smaller size and less rapidly expanding whorls (diameters of the first three whorls 0.80–0.85 mm, 1.5–1.6 mm, 2.35–2.50 mm respectively, versus c. 0.75 mm, c. 1.65 mm, c. 3.25 mm) The shell of *K. eurytrochus* is also distinctly thicker and less fragile.

Description. Shell small, rather thin, somewhat translucent or opaque, pale yellow-corneous to white. Surface shiny. Spire somewhat depressed-conical with approx. straight or slightly convex sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, last whorl angular at the periphery, rounded above and below the periphery. Sculpture. Protoconch with numerous fine, rather densely placed radial riblets, which are most distinct below the suture; numerous approx. equally strong, densely placed spiral grooves cutting into the crests of the radial riblets. Teleoconch. Radial sculpture: Growth lines at somewhat uneven intervals above the periphery, which are approx. as strong as the spiral sculpture, and which are most distinct just below the suture. Spiral sculpture: Last whorl with a peripheral spiral thread, above and below this numerous fine, moderately and evenly spaced, continuous grooves. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus closed. Dimensions. Height up to 2.65 mm; width up to 3.8 mm; diameters of the first four whorls 0.80–0.85 mm, 1.5–1.6 mm, 2.35–2.50 mm, 3.6–3.7 mm respectively; number of whorls up to 4 1/8; height aperture up to 1.5 mm; width aperture up to 2.0 mm.

Distribution in Sabah. Widespread but rare: Trus Madi range, Segaliud Lokan, Danum valley. Elevation range: 400–1100 m. In primary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Kaliella gregaria (Tillier & Bouchet, 1989)

(fig. 124d–f, 128b, map 26c)

Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 85. – *Gunongia gregaria* Tillier & Bouchet 1989 (1988): 264; Vermeulen 1996b: 288. – Type from Malaysia, Sabah, Kinabalu N.P.

Cross diagnosis. The spire expands more rapidly than in any other Borneo *Kaliella* (diameter of the first three whorls c. 0.75 mm, c. 1.65 mm, c. 3.25 mm respectively). In this respect, only *K. sublaxa* approaches *K. gregaria* (diameter of the first three whorls 0.7–0.8 mm, 1.35–1.50 mm, 2.40–2.65 mm respectively).

Description. Shell small, very thin, somewhat translucent, greenish or brownish. Surface shiny. Spire somewhat depressed-conical with straight sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, last whorl angular and slightly compressed at the periphery, rounded above and below the periphery. Sculpture. Protoconch with numerous fine, rather densely placed radial riblets; spiral sculpture subordinate to the radial sculpture and inconspicuous (visible at 40x magnification), numerous very densely placed grooves. Teleoconch. Radial sculpture: Above the periphery rather distinct, unevenly spaced, somewhat raised growth lines, next to these fine, densely and evenly placed (about as dense as the spiral grooves) riblets; below the periphery with similar but less distinct radial sculpture. Spiral sculpture: Last whorl with a peripheral thread, above and below this numerous continuous, fine, densely and evenly placed grooves. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus closed. Dimensions. Height up to 5.2 mm; width up to 6.8 mm; diameters of the first three whorls c. 0.75 mm, c. 1.65 mm, c. 3.25 mm respectively; number of whorls up to c. 4, height aperture up to 3.4 mm; width aperture up to 4 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2700–3500 m. In subalpine forest on diorite bedrock. Endemic to Sabah.

Kaliella sublaxa Vermeulen, Liew & Schilthuizen, 2015

(fig. 124g–i, map 26c)

Vermeulen et al. 2015: 87. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., km 54 marker on the road Kota Kinabalu-Tambunan, Gunung Mas.

Cross diagnosis. Differs from *Kaliella gregaria* by the more slowly expanding whorls (diameter of the third whorl 2.40–2.65 mm, versus c. 3.25 mm), and from *K. eurytrochus* by the denser spiral sculpture on the outer whorls, above the periphery, as well as by the larger aperture at the same number of whorls.

Resembles in general shape *K. dendrophila* (Group 1), differs by the protoconch sculpture with predominant radial riblets and the more convex outer whorls. Also resembles *K. calculosa* and *K. microsoma* (Group 4), differs

by the more rapidly expanding whorls (diameter of the third whorl 2.40–2.65 mm, versus 1.65–2.10 mm).

Description. Shell small, very thin, somewhat translucent, pale yellowish-brown. Surface shiny. Spire somewhat depressed-conical with straight or slightly concave sides; apex rounded. Whorls: Protoconch whorls rather flat, next whorls moderately convex, last whorl slightly angular, rounded above and below the periphery. Sculpture. Protoconch with numerous fine, densely placed radial riblets, spiral sculpture virtually absent. Teleoconch. Radial sculpture: Above the periphery with a few growth lines, next to these fine, densely and evenly placed (about as dense and as strong as the spiral grooves) riblets; below the periphery with similar but less distinct radial sculpture. Spiral sculpture: Last whorl with a thin peripheral thread, above and below this numerous fine, densely and evenly placed, continuous grooves. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus closed. Dimensions. Height up to 3.5 mm; width up to 4.1 mm; diameters of the first four whorls 0.7–0.8 mm, 1.35–1.50 mm, 2.40–2.65 mm, c. 3.9 mm respectively; number of whorls up to c. 4; height aperture up to 2.2 mm; width aperture up to 2.4 mm.

Distribution in Sabah. Highlands: Crocker range, Trus Madi range. Elevation range: 900–1700 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Group 3

Check also:

Kaliella calculosa (Group 4). See cross diagnosis with *K. dendrobates*.

Kaliella barrakporensis (Group 5). Rare specimens of *K. barrakporensis* may lack the peripheral thread. These differ from species in Group 3 by the more elongated conical spire and less conspicuous radial sculpture above the periphery.

Kaliella dendrobates (Tillier & Bouchet, 1989)

(fig. 125a–c, 128c, map 26d)

Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 104. – *Gunongia dendro-bates* Tillier & Bouchet 1989 (1988): 269; Vermeulen 1996b: 287. – Type from Malaysia, Sabah, Kinabalu N.P.

Kaliella c.f. scandens Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Differs from *Kaliella scandens* by the much thinner, more shiny shell. Above the periphery unevenly raised growth lines predominate, a fine sculpture of minute radial riblets and even finer spiral grooves is indistinct or entirely absent. In *K. scandens* raised growth lines are usually absent, and the finer sculpture is continuous. Juveniles of *K. dendrobates* with a peripheral keel differ from *K. calculosa* in having a more depressed-conical spire, and a radial sculpture dominated by rather prominent, unevenly spaced, raised growth lines.

Description. Shell small, very thin, somewhat translucent, (yellowish) brown. Surface shiny. Spire somewhat depressed-conical with straight sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, last whorl rounded at the periphery (angular in juveniles), rounded above and below the periphery. Sculpture. Protoconch with numerous fine, densely placed radial riblets; spiral sculpture subordinate to the radial sculpture, very fine (just visible at 40x magnification) to rather distinct, very densely placed grooves, locally present. Teleoconch. Radial sculpture: Above the periphery distinct, unevenly spaced and locally crowded, somewhat raised growth lines, next to these areas with fine, densely (slightly more dense than the spiral striation) and evenly placed riblets, on the outer whorls locally interrupted by approximately smooth areas; below the periphery with unevenly spaced, slightly raised growth lines only. Spiral sculpture: Above the periphery locally with fine, slightly spaced, narrow spiral grooves cutting into the crests of the radial riblets and subordinate to these, particularly towards the suture and the periphery; below the periphery slightly coarser and slightly more spaced spiral grooves. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, very narrow. Dimensions. Height up to 3.2 mm; width up to 3.9 mm; diameters of the first four whorls 0.65–0.75 mm, c. 1.1 mm, 1.7–1.8 mm, c. 2.65 mm respectively; number of whorls up to c. 5 1/2; height aperture up to 1.6 mm; width aperture up to 1.9 mm.

Animal with an obtuse caudal horn.

Radula. Central 1-cuspid; laterals and marginals similar, serrate with 2 large cones at the tip and a small in between

Distribution in Sabah. Highlands: Mount Kinabalu, Trus Madi range. Elevation range: 1600–3400 m. In montane and sub-alpine forest on granodiorite and sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Kaliella micula (Mousson, 1857), a widespread species which occurs in Sarawak, resembles *K. dendrobates* but has a widely rounded apex and slightly convex sides. The whorls expand more rapidly than in *K. dendrobates* (diameter of the first four whorls c. 1.0 mm, 1.7 mm, 2.8 mm, 4.0 mm respectively in a Sarawak specimen).

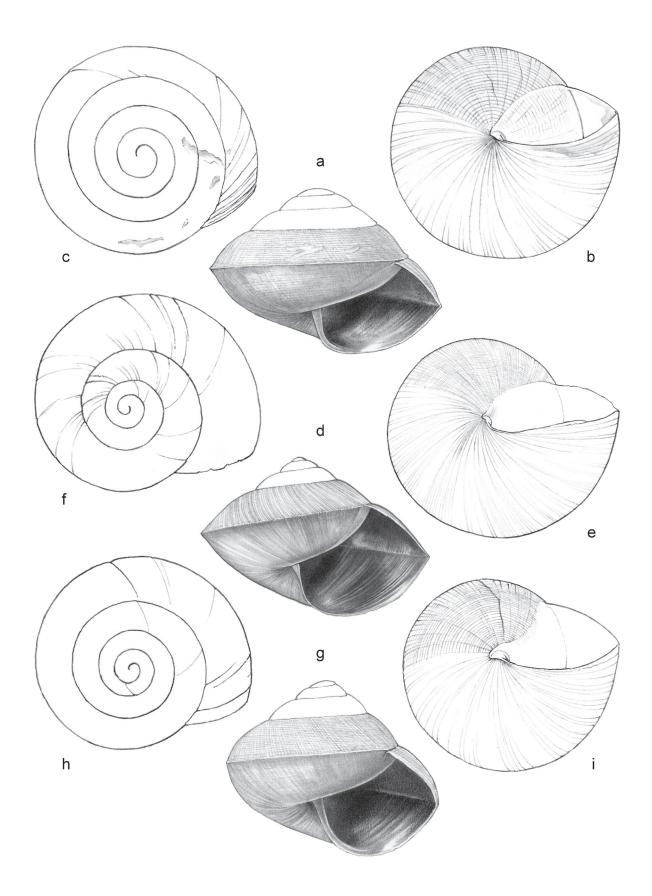


Fig. 124, a–c. *Kaliella eurytrochus* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 2.6 mm high, b. Umbilical view, c. Apical view; d–f. *Kaliella gregaria* (Tillier & Bouchet, 1989), d. Frontal view, shell 3.6 mm high, e. Umbilical view, f. Apical view; g–i. *Kaliella sublaxa* Vermeulen, Liew & Schilthuizen, 2015, g. Frontal view, shell 3.3 mm high, h. Umbilical view, i. Apical view.

Note. We depict a keeled, juvenile specimen of *K. dendrobates*, with approx. 1 whorl less than the type specimen. Adults do not have a keel.

Kaliella doliolum (L Pfeiffer, 1846)

(fig. 125d–e, map 26c)

Von Möllendorff 1890: 205; 1894: 207; Von Martens 1908: 261; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: 544, and online supplementary data; Vermeulen et al. 2015: 105; Phung et al. 2017: 86; Marzuki et al. 2021: 73. – *Helix doliolum* Pfeiffer 1846a: 41; Reeve 1851 (1851–1854): Pl. 43, fig. 196. – *Vitrinoconus doliolum* (L Pfeiffer) Pfeiffer & Clessin 1881: 33. – *Liardetia (Belopygmaeus) doliolum* (L Pfeiffer) Baker 1938: 27; Solem 1988: 549. – *Liardetia doliolum* (L Pfeiffer) Van Benthem Jutting 1950: 410; 1959: 138; Maassen 1997: 61; Vermeulen & Whitten 1998: 100, 151; Maassen 2001: 99; Tan et al. 2012: 105. – Type from Philippines, 'Sibonga, island of Zebu'.

Sitala (?) orchis Godwin-Austen 1891: 40. – Type from Malaysia, Sabah, Labuan.

Cross diagnosis. The shell shape resembles *Kaliella scandens*; diagnostic is the much coarser radial sculpture. If present, the spiral sculpture below the periphery is much finer.

Description. Shell small, rather thin, slightly translucent or opaque, (pale) brown. Surface with a silky luster. Spire somewhat depressed-conical with approx. straight sides; apex broadly rounded. Whorls: Protoconch whorls convex, next whorls (moderately) convex, last whorl rounded at the periphery (somewhat angular in juveniles), rounded above and below the periphery. Sculpture. Protoconch with numerous fine, densely placed radial riblets; spiral sculpture subordinate to the radial sculpture, very fine (just visible at 40x magnification), densely placed grooves cutting into the crests of the radial riblets. Teleoconch. Radial sculpture: Above the periphery with rather densely placed and somewhat unevenly spaced, distinct and rather coarse ribs; below the periphery with a few unevenly spaced, inconspicuous growth lines. Spiral sculpture: With or without subordinate, very fine and inconspicuous, rather dense spiral striation in the interstices of the radial ribs; below the periphery with or without fine, densely placed or somewhat spaced spiral grooves. Aperture semi-elliptic, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.9 mm; width up to 3.6 mm; diameters of the first four whorls 0.7–0.8 mm, 1.2–1.4 mm, 1.80–2.25 mm, 2.5–3.1 mm respectively; number of whorls up to c. 5 1/8; height aperture up to 0.7 mm; width aperture up to 1.2 mm.

Distribution in Sabah. Widespread and common in coastal areas and somewhat further inland; deep inland in Sapulut only. Elevation range: 0–400 m. In primary forest, secondary forest and coastal forest, on limestone bedrock and volcanic bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Vietnam, Malaysia (Peninsula), Singapore, Indonesia (S-wards to Java), E-wards to Australia, Pacific.

Kaliella scandens (Cox, 1872)

(fig. 125f–g, map 26d)

Schilthuizen et al. 2002: 256; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 101; Phung et al. 2017: 71; Foon et al. 2018: 96; Marzuki et al. 2021: 74. – Helix scandens Cox 1872 (1871): 645. – Hyalina (Conulus) scandens (Cox) Pfeiffer & Clessin 1881: 74. – Liardetia scandens (Cox) Solem 1988: 550; Vermeulen & Whitten 1998: 102, 151; Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen. 2003a: 96; Schilthuizen et al. 2003b: 41, 42. – Type from Australia, New South Wales, 'Port Macquarie'.

Kaliella indifferens Boettger 1891: 256. – Liardetia indifferens (O Boettger) Van Benthem Jutting 1950: 408; 1959: 138; Saul 1967: 109; Maassen 1997: 61; 2001: 99; Tan et al. 2012: 106. – Type from Indonesia, Ambon. Sitala dulcis Smith 1895: 111; Von Martens 1908: 261. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Description. Shell small, rather thin, somewhat translucent, (pale) brown, sometimes white. Surface with a silky luster. Spire somewhat depressed-conical with straight to slightly convex sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, last whorl rounded at the periphery (somewhat angular in juveniles), rounded above and below the periphery. Sculpture. Protoconch with numerous fine, rather densely placed radial riblets; spiral sculpture subordinate to the radial sculpture or approx. equally distinct, very fine (just visible at 40x magnification), densely placed grooves. Teleoconch. Radial sculpture: Above the periphery fine, densely and evenly placed riblets; below the periphery with a few unevenly spaced, inconspicuous growth lines only. Spiral sculpture: Above the periphery with fine, slightly spaced, narrow grooves cutting into the crests of the radial riblets and subordinate to these; below the periphery slightly coarser and slightly more spaced grooves. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, very narrow. Dimensions. Height up to 2.8 mm; width up to 3.65 mm; diameters of the first four whorls 0.6–0.7 mm, 1.05–1.30 mm, 1.6–1.9(–2.0) mm, 2.25–2.70(–3.0 mm) respectively; number of whorls up to c. 5 1/2; height aperture up to 0.7 mm; width aperture up to 1.2 mm.

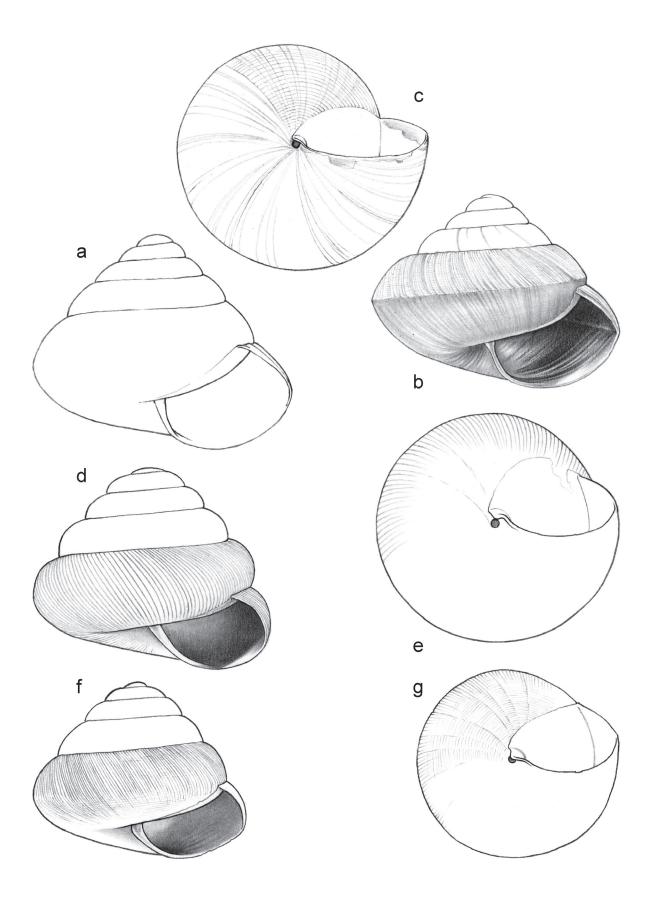


Fig. 125, a–c. *Kaliella dendrobates* (Tillier & Bouchet, 1989), frontal views, a. Shell 4 mm high, b. Shell 2.6 mm high; c. Umbilical view; d–e. *Kaliella doliolum* (L Pfeiffer, 1846), d. Frontal view, shell 2.5 mm high, e. Umbilical view; f–g. *Kaliella scandens* (Cox, 1872), f. Frontal view, shell 2.2 mm high, g. Umbilical view.

Radula. Central 3-cuspid; laterals 3-cuspid; marginals 3-5 cuspid.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary and secondary forest, coastal forest. Also in Sarawak, Kalimantan. Distribution elsewhere: Vietnam, Thailand, Malaysia (Peninsula), Singapore, Indonesia (S-wards to Java), E-wards to Australia, Pacific.

Variability. Samples from montane environments include shells with a more rapidly expanding spire than usual (diameter of the fourth whorl up to 3.0 mm; in other specimens 2.25–2.70 mm). In this character the shells approach *Kaliella dendrobates*, but the sculpture is typical for *K. scandens*.

Group 4

Kaliella calculosa (Gould, 1852)

(fig. 121f, 126a-c, 128d, map 26e)

Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 93; Phung et al. 2017: 89; Marzuki et al. 2021: 72. – Helix calculosa Gould 1852: 48. – Trochomorpha (Nigritella) calculosa (Gould) Pfeiffer & Clessin 1881: 79. – Coneuplecta (Durgellina) calculosa (Gould) Baker 1941: 234; Solem 1988: 544. – Type from Society islands, Tahiti.

Sitala demissa Smith 1895: 110; Von Martens 1908: 261. – Type from Malaysia, Sarawak 'Mulu mountains and Busau'.

Coneuplecta sitaliformis auct. Schilthuizen et al. 2002: 256.

Kaliella sp. 1 Uchida et al. 2013: 53, 54.

[Not Kaliella sitaliformis Von Möllendorff].

Cross diagnosis. Fresh shells are thinner and more translucent than the other species in Group 4. Shells of *Kaliella dendrophila* (Group 1) are also thin and translucent but differ by having a sculpture consisting of tiny beads. Juveniles can be distinguished by the different apical sculpture. Juveniles also resemble *K. dendrobates* (Group 3), see there.

Description. Shell small, very thin, translucent, pale yellow-green to pale yellow-brown. Surface with a silky luster, shiny below the periphery. Spire conical with about straight sides. Whorls somewhat convex, last whorl almost rounded to angular at the periphery, moderately convex below the periphery. Sculpture. Protoconch with distinct, fine, densely placed radial riblets; spiral sculpture slightly subordinate, equally densely placed or slightly more spaced grooves cutting into the crests of the radial riblets. Teleoconch. Radial sculpture subordinate to the spiral sculpture: Above the periphery inconspicuous growth lines, next to these very fine, densely and evenly placed riblets, sometimes on the outer whorls locally interrupted by approximately smooth areas; below the periphery with occasional growth lines only. Spiral sculpture: Last whorl with or without a thin peripheral spiral thread, above and below the periphery with very fine to rather coarse, moderately to widely spaced, continuous, sometimes rather shallow and wide grooves cutting through the radial riblets. Aperture approx. semi-elliptic, peristome not widened, not thickened. Umbilicus open, very narrow. Dimensions. Height up to 5.0 mm; width up to 4.6 mm; diameters of the first four whorls 0.65–0.75 mm, 1.15–1.25 mm, 1.75–2.10 mm, 2.6–3.2 mm respectively; number of whorls up to c. 5 3/4; height aperture up to 2.5 mm; width aperture up to 2.7 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2100 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Distribution elsewhere: From India, Laos, to Australia; E-wards to Tahiti. Similar species elsewhere. Kaliella sitaliformis Von Möllendorff, 1897 (Indonesia: Java, Bali, and Sulawesi); see illustration in Vermeulen & Whitten (1998: 99), differs by having a raised spiral sculpture, visible in between the radial riblets, on the outer whorls.

Variability. Kaliella calculosa is variable in the prominence and the density of the spiral sculpture on the teleoconch. SEM-images show that the widest spiral grooves have a distinctly convex bottom; it is as if a thin thread is embedded in the groove.

Kaliella microsoma Vermeulen, Liew & Schilthuizen, 2015

(fig. 126d-e, map 26f)

Vermeulen et al. 2015: 95. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., km 54 marker on the road Kota Kinabalu-Tambunan, Gunung Mas.

Cross diagnosis. Resembles juvenile Kaliella calculosa, differs by the more convex whorls. General shape as K. gregaria (Group 2), but smaller and with whorls less rapidly expanding (diameter of first three whorls 0.45–0.55 mm, 1.0–1.2 mm, 1.65–1.90 mm respectively, versus c. 0.75 mm, c. 1.65 mm, c. 3.25 mm), with a slightly higher conical spire and with more convex whorls. The spiral sculpture is generally coarser than in K. gregaria but may be inconspicuous in specimens from the Crocker range (including the illustrated shell which, on the lower

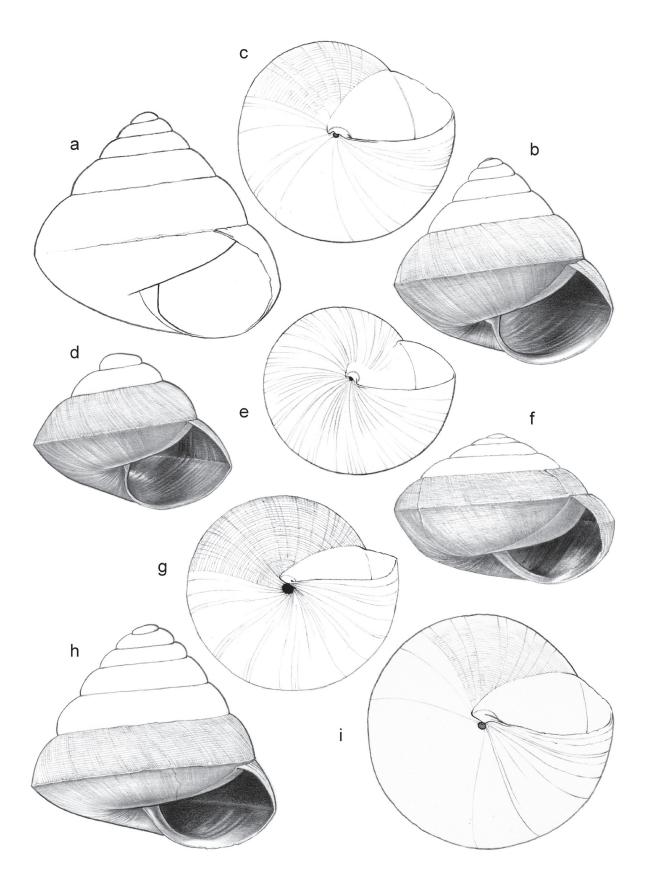


Fig. 126, a–c. *Kaliella calculosa* (Gould, 1852), frontal views, a. Shell 4 mm high, b. Shell 3.6 mm high; c. Umbilical view; d–e. *Kaliella microsoma* Vermeulen, Liew & Schilthuizen, 2015, d. Frontal view, shell 1.6 mm high, e. Umbilical view; f–g. *Kaliella phacomorpha* Vermeulen, Liew & Schilthuizen, 2015, f. Frontal view, shell 1.8 mm high, g. Umbilical view; h–i. *Kaliella punctata V*ermeulen, Liew & Schilthuizen, 2015, h. Frontal view, shell 4.5 mm high, i. Umbilical view.

surface, has spiral sculpture only near the aperture).

Description. Shell very small, very thin, somewhat translucent, greenish-brown. Surface with a silky luster. Spire conical with slightly convex sides; apex rounded. Whorls: Top whorls convex, outer whorls only a little less convex, last whorl angular at the periphery, somewhat obtusely so near the aperture in adult specimens, moderately convex below the periphery. Sculpture. Protoconch with very fine, densely placed radial riblets; spiral sculpture subordinate to the radial sculpture and sometimes inconspicuous, very densely placed grooves, just visible at 40x magnification. Teleoconch. Radial sculpture: Above the periphery rather inconspicuous, unevenly spaced, somewhat raised growth lines; next to these fine, very densely and evenly placed riblets on the inner whorls, less densely placed riblets locally present on the outer whorls; radial sculpture less conspicuous below the periphery. Spiral sculpture: Last whorl with a peripheral thread, above the periphery with fine, moderately spaced, narrow grooves that cut into the crests of the radial riblets and that are slightly to distinctly subordinate to these; below the periphery with similar, but slightly more distinct and slightly more spaced grooves. All spiral sculpture varies from rather distinct to inconspicuous and only locally present. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, very narrow, or closed. Dimensions. Height up to 1.6 mm; width up to 1.8 mm; diameters of the first three whorls 0.45–0.55 mm, 1.0–1.2 mm, 1.65–1.90 mm respectively; number of whorls up to c. 3 3/8; height aperture up to 0.85 mm; width aperture up to 1.0 mm.

Distribution in Sabah. Highlands: Crocker range, Upper Padas. Elevation range: 1100–1400 m. In primary forest on sandstone/shale bedrock. Endemic to Sabah.

Kaliella phacomorpha Vermeulen, Liew & Schilthuizen, 2015

(fig. 126f–g, map 27a)

Vermeulen et al. 2015: 90. – Type from Malaysia, Sabah, Interior Prov., mount Trus Madi slopes, Gua Loloposon.

Cross diagnosis. Uniquely identified among Sabah Kaliella species by its depressed-conical, almost lenticular

Cross diagnosis. Uniquely identified among Sabah Kaliella species by its depressed-conical, almost lenticular spire.

Description. Shell very small, rather thin, somewhat translucent or opaque, yellow-brown corneous. Surface shiny. Spire depressed-conical to almost lenticular with slightly convex sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, the last whorl angular at the periphery, rounded above and below the periphery. Sculpture. Protoconch with numerous fine, densely placed radial riblets; spiral sculpture subordinate to the radial sculpture, consisting of approx. 12 very fine, densely placed spiral grooves cutting into the crests of the radial riblets. Teleoconch. Radial sculpture: Growth lines above the periphery only. Spiral sculpture: Last whorl with a peripheral thread, above and below this, numerous continuous, fine, evenly spaced, continuous grooves. Aperture crescent-shaped, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 1.7 mm; width up to 2.6 mm; diameters of the first four whorls 0.55–0.65 mm, 0.95–1.10 mm, 1.45–1.60 mm, 2.05–2.30 mm respectively; number of whorls up to 4 3/4; height aperture up to 1.05 mm; width aperture up to 1.3 mm.

Distribution in Sabah. Highlands: Crocker range, Trus Madi range. Elevation range: 900–1200 m. Found in primary forest on limestone bedrock. Endemic to Sabah.

Kaliella punctata Vermeulen, Liew & Schilthuizen, 2015

(fig. 121e, 126h-i, 128e, map 27b)

Vermeulen et al. 2015: 91. – Type from Malaysia, Sabah, Interior Prov., Sapulut river valley, Gua Pungiton. *Kaliella punctata*, unavailable name, Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data.

Liardetia angulata auct. Saul 1967: 109.

Coneuplecta angulata auct. Schilthuizen et al. 2002: 256, 257; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Clements et al. 2008: 2762.

[Not Trochomorpha angulata Issel].

Cross diagnosis. Uniquely identified among Sabah *Kaliella* by the pitted spiral sculpture on the teleoconch, in combination with its size. In *K. dendrophila* (Group 1), the spiral sculpture consists of beads on the shell surface. It is much smaller, has a thinner, more translucent shell with a smaller protoconch with predominant spiral sculpture, and with whorls more rapidly expanding.

Description. Shell (very) small, thin, slightly translucent or approx. opaque, pale (yellowish) brown. Surface shiny. Spire conical with straight or slightly convex sides; apex rounded. Whorls: Protoconch whorls convex, next whorls moderately convex, the last whorl angular at the periphery, rounded above and below the periphery. Sculpture. Protoconch with fine, densely placed but slightly unevenly spaced radial riblets; spiral sculpture about equally strong, fine, slightly more spaced grooves which are partly continuous, and partly broken up into minute pits. Teleoconch. Radial sculpture: Above the periphery with some unevenly spaced, somewhat raised growth

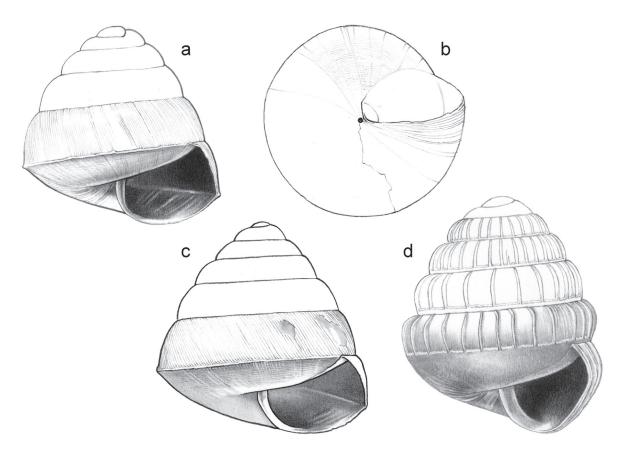


Fig. 127, a–b. *Kaliella accepta* (E A Smith, 1895), a. Frontal view, shell 2.5 mm high, b. Umbilical view; c. *Kaliella barrak-porensis* (Reeve, 1852), frontal view, shell 2.5 mm high; d. *Rahula delopleura* Vermeulen, Liew & Schilthuizen, 2015, frontal view, shell 2.5 mm high.

lines, these less conspicuous below the periphery. Spiral sculpture: Last whorl with or without a peripheral spiral thread, above the periphery with numerous (rather) fine, well-spaced grooves which consist of rows of densely placed pits which are often elongated in the direction of the growth lines; below the periphery usually with numerous fine, well-spaced, continuous grooves. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, very narrow. Dimensions. Height up to 6 mm; width up to 5.4 mm; diameters of the first four whorls 0.7-1.0 mm, 1.15-1.60 mm, 1.7-2.2 mm, 2.1-3.2 mm respectively; number of whorls up to 7.7/8; height aperture up to 2.1 mm; width aperture up to 3 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–3400 m. In primary and secondary forest on limestone, sandstone/shale, and granodiorite bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Indonesia (Sulawesi).

Variability. The spiral sculpture above the periphery is fine in some specimens, somewhat coarser in others. The continuous spiral striation below the periphery is absent in some specimens.

Group 5

Kaliella accepta (E A Smith, 1895)

(fig. 121b, 127a-b, 128f, map 27c)

Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 99. – *Sitala accepta* Smith 1895: 111; Von Martens 1908: 261. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill, and Philippines, 'Palawan'.

Liardetia 'sp. bo-01' Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42.

Cross diagnosis. Adult or nearly adult shells differ from *Kaliella barrakporensis* by the more depressed-conical spire with more convex sides and a more broadly rounded apex. Usually, the sculpture is less distinct than in *K. barrakporensis*, and the shells are glossier. Juveniles of both species are sometimes difficult to keep apart.

Description. Shell small, rather thin, somewhat translucent or opaque, (pale) yellow-corneous to brown-corneous. Surface glossy or shiny. Spire (somewhat depressed) conical with convex sides; apex broadly rounded. Whorls: Protoconch whorls convex, others moderately convex, the last whorl approx. angular at the periphery, rounded above, rounded to almost flat below the periphery. Sculpture. Protoconch with spaced radial riblets and usually subordinate (sometimes equally distinct), very fine spiral grooves; usually these are reduced to spiral rows of minute, shallow indentations; often the protoconch is almost smooth. Teleoconch. Radial sculpture: Above the periphery very fine, inconspicuous, densely and evenly placed riblets locally, or with a few growth lines only; below the periphery approx. absent. Spiral sculpture: Last whorl with a peripheral thread which starts at the level of the suture of the penultimate whorl, with or without traces of very fine, inconspicuous striation, below the periphery usually with numerous fine, moderately and evenly spaced, continuous grooves which are most distinct towards the periphery. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.8 mm; width up to 3.2 mm; diameters of the first four whorls 0.5–0.8 mm, 0.90–1.35 mm, 1.5–2.0 mm, 2.0–2.8 mm respectively; number of whorls up to 5; height aperture up to 1.2 mm; width aperture up to 1.6 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary and secondary forest on limestone, sandstone/shale and volcanic bedrock. Also in Kalimantan. Endemic to Borneo.

Kaliella barrakporensis (Reeve, 1852)

(fig. 127c, map 27d)

Godwin-Austen 1882 (1882–1888): 2; Naggs & Raheem 1999: iv, 28; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 96; Phung et al. 2017: 89; Marzuki et al. 2021: 71. – Helix barrak-porensis Reeve 1852 (1851–1854): Pl. 132, fig. 816; Pfeiffer 1853: 59; 1854 (1852a): 156. – Trochomorpha (Kaliella) barrakporensis (Reeve) Pfeiffer & Clessin 1881: 83. – Type from India, 'Barrakpore'.

Sitala rumbangensis Smith 1895: 110; Von Martens 1908: 261. – Schwammeria rumbangensis (E A Smith) Schileyko 2010: 6. – Type from Malaysia, Sarawak 'Rumbang and mount Rabong'.

Sitala cara Smith 1895: 111; Von Martens 1908: 261. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Gomantong hill.

Sitala busauensis Smith 1895: 111. – Liardetia busauensis (Smith) Saul 1967: 109. – Type from Malaysia, Sarawak, 'Busau'

Kaliella angigyra Von Möllendorff 1897: 60. – *Liardetia angigyra angigyra* (Von Möllendorff) Van Benthem Jutting 1950: 398; 1959: 137; Vermeulen & Whitten 1998: 100, 151; Maassen 2001: 98; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 257, 258. – Type from Indonesia, Java.

Kaliella sp. 2 Uchida et al. 2013: 53, 54.

Description. Shell small, rather thin, somewhat translucent or opaque, (pale) brown-corneous. Surface shiny or with a silky luster. Spire (somewhat elongated) conical with almost flat or slightly convex sides; apex narrowly rounded. Whorls: Protoconch whorls convex, others moderately convex, the last whorl rounded to angular at the periphery, rounded above and below the periphery. Sculpture. Protoconch with spaced, inconspicuous radial riblets and usually subordinate, very fine spiral grooves; protoconch sometimes almost smooth. Teleoconch. Radial sculpture: Above the periphery very fine, densely and evenly placed riblets, often only locally present, in some specimens virtually absent; below the periphery approx. absent. Spiral sculpture: Last whorl usually with a peripheral thread which starts at the level of the suture of the penultimate whor, and with or without traces of very fine (just visible at 40x magnification), inconspicuous striation; below the periphery usually with numerous fine, moderately and evenly spaced, continuous grooves. Aperture obtusely trapezoid, peristome not widened, not thickened. Umbilicus open, narrow, or almost closed. Dimensions. Height up to 4.6 mm; width up to 4.3 mm; diameters of the first four whorls 0.65–0.80 mm, 1.10–1.25 mm, 1.5–2.0 mm, 2.15–2.70 mm respectively; number of whorls up to 6 1/2; height aperture up to 1.5 mm; width aperture up to 2.0 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–2200 m. In primary and secondary forest, in rocky, vegetated roadsides, on limestone, sandstone, and granodiorite bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Similar shells (but see note) are known from Africa. India, Sri Lanka, Thailand, Laos, Malaysia (Peninsula), Indonesia (S-wards to Java, E-wards to Sulawesi, Flores).

Variability. Some specimens lack the spiral thread along the periphery of the last whorl. A fine but almost continuous spiral striation may be present on the top whorls.

Note. The genus Schwammeria Schileyko, 2010 is based on animals found living in the Vienna Zoo, possibly



Fig. 128, a. *Kaliella microconus* (Mousson, 1865); b. *Kaliella gregaria* (Tillier & Bouchet, 1989); c. *Kaliella dendrobates* (Tillier & Bouchet, 1989); d. *Kaliella calculosa* (Gould, 1852); e. *Kaliella punctata* Vermeulen, Liew & Schilthuizen, 2015; f. *Kaliella accepta* (E A Smith, 1895).

originating from Kalimantan. These, identified as the type species *rumbangensis*, are anatomically distinct from Sri Lanka material of *Kaliella barrakporensis*, but the shells are very similar. *Kaliella barrakporensis* in our sense may be a composite of species with similar shells but of different affinity; further investigation is needed.

Genus Rahula Godwin-Austen, 1907

Diagnosis for the Sabah species. Radial sculpture teleoconch approx. orthocline, consisting of widely spaced, coarse ribs. Last whorl with 1 spiral thread near the periphery.

Notes. 1. In extralimital species of the genus prosocline radial ribs predominate.

2. Placed in Ariophantidae in MolluscaBase (accessed 1/2021). Our placement in Chronidae is based on shell similarity.

The latest on the genus can be found in Foon & Marzuki (2020), Gittenberger et al. (2017a, 2017b, 2021).

Rahula delopleura Vermeulen, Liew & Schilthuizen, 2015

(fig. 127d, map 27e)

Vermeulen 2015: 107. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Batu Pangi. *Rahula raricostulata* auct. Schilthuizen & Vermeulen 2003a: 96.

Rahula 'sp. 1' Clements et al. 2008: 2762.

[Not Sitala raricostulata E A Smith].

Description. Shell small, rather solid, somewhat translucent to opaque, (pale) brown. Surface shiny. Spire conical with convex sides to almost ovoid; apex rounded. Whorls convex, rounded, suture somewhat impressed. Sculpture. Protoconch with very fine, densely placed radial riblets starting at some distance from the apex; apex with very fine (just visible at 40x magnification), inconspicuous spiral striation, which gradually disappears where the radial riblets become more prominent. Teleoconch. Radial sculpture: Above the periphery consisting of well-spaced (26–33 on the last whorl), coarse, orthocline, approx. straight, high and narrow ribs, which connect to a spiral ridge around the periphery, interstices smooth or with an occasional, inconspicuous growth line. Spiral sculpture: Last whorl with a distinct spiral ridge slightly below the periphery, which seems to be the edge of a callus covering the lower surface of the shell, and which continues just above the suture of the penultimate whorl; next to this a fine, dense spiral striation on the lower surface of the shell. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus closed. Dimensions. Height up to 2.6 mm; width up to 2.1 mm; diameters of the first four whorls 0.5–0.6 mm, 0.8–0.9 mm, 1.1–1.2 mm, 1.35–1.55 mm respectively; number of whorls up to 6 1/2; height aperture up to 0.85 mm; width aperture up to 1.1 mm.



Fig. 129. *Phaedusa filicostata filialis* (E Von Martens, 1903), frontal view, shell 25.5 mm high.

Distribution in Sabah. Scattered localities in E; elsewhere in Sinobang and Sapulut only. Elevation range: 0–500 m. In primary and secondary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. Differs from Rahula raricostulata (E A Smith, 1893), from Sarawak, by the absence of a distinct, predominant spiral sculpture on the protoconch. Rahula raricostulata also has a more conical spire, and fewer radial ribs (11–20) on the last whorl.

Family **CLAUSILIIDAE** Gray, 1855

Diagnosis for the Sabah species. Snails. Shell with 10 3/8–11 3/4 slowly expanding whorls. Shell sinistral, large, much higher than wide, fusiform; last whorl approx. flat. Teleoconch sculpture: Radial sculpture consisting of uneven, fine riblets, spiral sculpture absent. Aperture with teeth. Peristome on the palatal side not thickened, spreading. Umbilicus closed. Dimensions: Adults 25.5–27.2 mm high, 4.8–5.1 mm wide.

Genus *Phaedusa* H & A Adams, 1855

Phaedusa filicostata filialis (E Von Martens, 1903) (fig. 129, map 27f)

Loosjes 1953: 50; Schilthuizen et al. 2003b: 42; Clements et al. 2008: 2761. – *Clausilia filialis* Von Martens 1903: 425 ('*Clunsilia*'); 1908: 263, 287. – Type from Indonesia, Kalimantan, 'Gunung Sekerat'.

Phaedusa filicostata auct. Schilthuizen et al. 2002: 256. Phaedusa sp. Schilthuizen & Rutjes 2001: 420. [Not Clausilia filicostata Stoliczka].

Description. Shell large, thin, opaque, greyish brown, white just below the suture. Surface dull. Spire narrowly fusiform, apex slightly protruding, rounded. Whorls: Protoconch whorls convex; first teleoconch whorl moderately convex, grading to an almost flat penultimate whorl. Sculpture. Radial sculpture: Fine, densely placed and somewhat unevenly spaced riblets. Spiral striation absent. Aperture ovate, narrowly rounded above; apertural teeth 2: one short parietalis, one long, curved columellaris continuing deep inside the shell, there with a loose lamella (clausilium) lying close to it and following its curvature; approx. 1/2 whorl from the aperture with 8 more longitudinal lamellae in palatal position, the upper very long, parallel to and close to the suture, the one below shorter and with its posterior end downwards oblique, the others short, those towards the basis increasingly downwards oblique, the lowermost opposite the clausilium. Peristome dull white, somewhat thickened, spreading, free on the parietal side. Umbilicus closed. Dimensions. Height 25.5–27.2 mm; width 4.8–5.1 mm; ratio height/width 5.0–5.7; number of whorls 10 3/8–11 3/4; height aperture 6.0–6.2 mm; width 4.3–4.5 mm.

Distribution in Sabah. Rare in E: Danum valley, Ulu Segama. Elevation range: 0–300 m. Primary and secondary forest on limestone and sandstone/shale bedrock. Also in Kalimantan. Endemic to Borneo.

Family **DIAPHERIDAE** Panha & Naggs, 2010

Diagnosis for the Sabah species. Snails. Shell with 5 7/8–10 slowly expanding whorls. Shell dextral, small, higher than wide, spire subcylindrical to ellipsoid(-cylindrical) to (ob-)ovoid; last whorl angular below, last part detached or not. Teleoconch sculpture: Radial sculpture next to varices consisting subsutural crenulations locally developing into radial ribs, spiral sculpture absent, or inconspicuous. Aperture with teeth. Peristome on the palatal side thickened, spreading. Umbilicus closed or open, narrow or wide. Dimensions: Adults 5.0–8.7 mm high, 1.1–4.7 mm wide.

Note. See Páll-Gergely et al. 2020b for a generic overview of the family.

Genus *Diaphera* Albers, 1850

Diagnosis for the Sabah species. Last 1/4 to 1/2 whorl (the tuba) detached from the spire, pointing obliquely downwards. Spire with varices. Umbilicus open.

Variability. In both species, specimens occur with an exceptionally short and wide spire. Such specimens may obfuscate the differences between the species and are best excluded at a first attempt to identification of series of shells.

Notes. 1. At several stages, juveniles develop a thickened peristome with apertural teeth. The teeth are different from those in adult shells: One angularis, one columellaris, and two basales. All are situated close to the peristome. Peristome and teeth are only partly resorbed when the animal resumes growth; the thickened peristome remains visible in the outer shell wall as a radial ridge (varix).

2. The Borneo species are revised in Vermeulen (1990).

Diaphera helenae Vermeulen, 1990

(fig. 130a-b, map 28a)

Vermeulen 1990: 161. – Type from Malaysia, Sabah, Tawau Prov., Baturong-Madai F.R., Madai hill.

Cross diagnosis. Differs from *Diaphera wilfordi* by the larger whorl count (8 1/4–10 whorls, versus 5 7/8–7 3/8 whorls), and usually by its longer spire (height minus last whorl 5.0–7.1 mm, versus 2.5–5.5 mm).

Description. Shell small, thin, opaque to slightly translucent, white. Surface shiny. Spire ellipsoid-cylindrical to obovoid, apex rounded. Whorls convex; suture impressed. Sculpture. Protoconch with a slight, minute radial as well as spiral striation. Teleoconch with distinct crenulations below the suture which often continue as rather inconspicuous, well-spaced, thin, rounded radial ribs, most conspicuously present on the first whorls and the last whorl, particularly close to the aperture. Spire with 3–4 varices in the apical half. Spiral sculpture: An inconspicuous striation locally present. Aperture approx. circular or obliquely ovate. Peristome thickened, particularly along the palatal side, and spreading, receding on the upper palatal side. Apertural teeth 3: 1 prominent angularis starting on the peristome, reaching deep inside, 1 short palatalis deep inside the aperture, 1 columellaris starting deep inside the aperture and reaching even deeper. Umbilicus open, wide, last whorl with a sharp basal ridge. Dimensions. Height 6.8–8.7 mm; height minus last whorl 5.0–7.1 mm; width 2.5–3.3 mm; height (minus last whorl)/width

2.0-2.3; number of whorls 8 1/4-10, height aperture 1.4-1.8 mm; width aperture 1.4-1.8 mm.

Distribution in Sabah. Rare in E: Ulu Segama, Baturong-Madai. Elevation range: 100–200 m. Lowland forest on and around limestone bedrock. Endemic to Sabah.

Diaphera wilfordi wilfordi Dance, 1970

(fig. 130c, map 28a)

Diaphera wilfordi Dance 1970: 157; Vermeulen 1990: 163; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96. – Type from Malaysia, Sabah, Tabin river.

Description. Shell small, thin, opaque to slightly translucent, white. Surface shiny. Spire fusiform to (ob-) ovoid, or about cylindrical when 3 mm wide or wider, apex rounded. Whorls convex; suture impressed. Sculpture. Protoconch approx. smooth. Teleoconch largely smooth, with distinct crenulations below the suture which only locally continue as a few inconspicuous, well-spaced, thin, rounded radial ribs, most distinctly so towards the base of the last whorl and close to the aperture. Spire with 2–3 varices in the apical half. Spiral sculpture absent. Aperture obliquely ovate. Peristome thickened, particularly along the palatal side, and spreading, receding on the upper palatal side. Apertural teeth 3: 1 prominent angularis starting on the peristome, reaching deep inside, 1 short palatalis deep inside the aperture, 1 columellaris starting deep inside the aperture and reaching even deeper. Umbilicus open, wide, last whorl with a sharp basal ridge. Dimensions. Height 5.3–7.8 mm; height minus last whorl 2.5–5.5 mm; width 2.3–3.1 mm; height (minus last whorl)/width 1–1.96; number of whorls 5 7/8–7 3/8, height aperture 1.3–1.7 mm; width aperture 1.4–1.8 mm.

Distribution in Sabah. Rare in N and E: Banggi and Balambangan islands, Tabin. Elevation range: 0–100 m. Lowland forest and coastal forest on limestone bedrock. Endemic to Sabah.

Variability. The Tabin population consists of small, relatively narrow shells (height minus tuba 2.5–4.2 mm, width 2.5–2.8 mm) which show less variability than the populations on the islands. The island populations include shells resembling the Tabin population next to shells that are larger and wider, in width overlapping with subsp. *ectyphus.* Shells 3 mm wide or wider usually differ from subsp. *ectyphus* in being more cylindrical. A few individuals, however, are impossible to identify without knowing the provenance.

Diaphera wilfordi ectyphus Vermeulen, 1990

(fig. 130d, map 28b)

Vermeulen 1990: 164; Clements et al. 2008: 2762. – Type from Malaysia, Sabah, Tawau Prov., Lahad Datu, Kirk's Cave.

Cross diagnosis. Differs from the type subspecies by the wider shell (3.0–3.3 mm wide, versus 2.3–3.1 mm), in combination with the ellipsoid to ovoid spire, versus fusiform to (ob-)ovoid, or about cylindrical when 3 mm wide or wider.

Description. Spire ellipsoid to ovoid. Dimensions. Height 5.6–7.2 mm; height minus last whorl 3.6–4.7 mm; width 3.0–3.3 mm; height (minus last whorl)/width 1.20–1.53; number of whorls 5 7/8–7 3/8, height aperture 1.5–1.9 mm; width aperture 1.6–2.0 mm.

Distribution in Sabah. Scattered localities in E: Lower Kinabatangan, Sabahmas, Ulu Segama, Danum valley. Elevation range: 0–200 m. Lowland forest and coastal forest on limestone bedrock. Endemic to Sabah.

Genus Gulella L Pfeiffer, 1856

Diagnosis for the Sabah species. Last whorl entirely connected to the spire. Spire without varices. Umbilicus closed.

Gulella bicolor (T Hutton, 1834)

(fig. 130e, 131, map 28c)

Van Benthem Jutting 1941: 320; Cowie 1997: 31; Vermeulen & Whitten 1998: 91, 148; Vermeulen 2007: 174; Schilthuizen et al. 2011: 5; Tan et al. 2012: 101; Schilthuizen et al. 2013: Online supplementary data; Marzuki et al. 2021: 48. – *Pupa bicolor* Hutton 1834: 86, 93; Pfeiffer 1848b: 352. – *Ennea bicolor* (T Hutton) Pfeiffer 1859 (1854–1860): 115; Issel 1874: 414; Von Martens 1908: 263. – *Ennea (Huttonella) bicolor* (T Hutton) Pfeiffer 1855b: 169; Stoliczka 1871: 169; Pfeiffer & Clessin 1881: 20. – *Gulella (Huttonella) bicolor* (T Hutton) Van Benthem Jutting 1950: 504. – *Huttonella bicolor* (T Hutton) Van Benthem Jutting 1959: 172; 1964: 69; Saul 1967: 109; Dance 1970: 153; Maassen 2001: 94; Clements et al. 2008: 2762; Phung et al. 2017: 90. – Type from India, 'Mirzapoor'.

Description. Shell small, thin, somewhat translucent, white. Surface glossy. Spire subcylindrical, slightly ta-

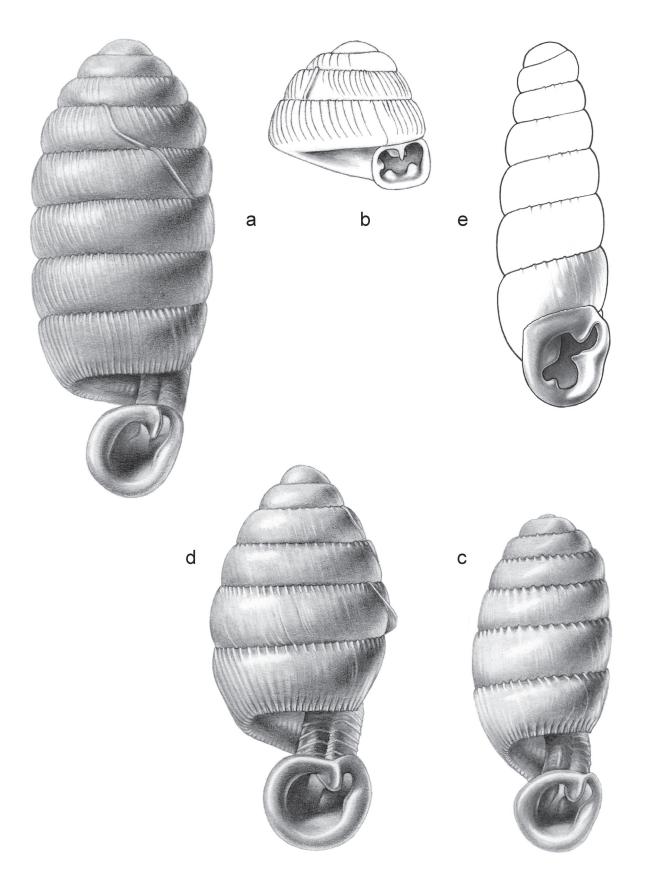


Fig. 130, a–b. *Diaphera helenae* Vermeulen, 1990, a. Frontal view, shell 8.8 mm high, b. Juvenile, frontal view, shell 2.8 mm high; c. *Diaphera wilfordi wilfordi* Dance, 1970, frontal view, shell 6.5 mm high; d. *Diaphera wilfordi ectyphus* Vermeulen, 1990, frontal view, shell 7.4 mm high; e. *Gulella bicolor* (T Hutton, 1834), frontal view, shell 5.5 mm high.



Fig. 131. Gulella bicolor (T Hutton, 1834).

pering towards the apex, sides slightly convex, apex broadly rounded. Whorls convex; suture moderately impressed. Sculpture. Protoconch smooth. Teleoconch smooth, apart from distinct crenulations below the suture which develop into low, rounded, well-spaced radial ribs on the last portion of the last whorl. Spire without varices. Spiral sculpture absent. Aperture sub-rectangular with rounded edges, with 2 indentations on the palatal side, just behind the aperture, corresponding with apertural teeth. Peristome a rather thin glazing on the parietal side, elsewhere thickened and spreading, only slightly receding on the upper palatal side. Apertural teeth 4: 1 prominent, short angularis starting on the peristome, 1 conical palatalis on the inner edge of the peristome, 1 basalis deeper inside, 1 columellaris starting close to the peristome and continuing deep inside. Umbilicus closed. Dimensions. Height 5.0-7.0 mm; width 1.1-2 mm; ratio height/width 3.3–4.6; number of whorls 6 1/8-8 1/2, height aperture 1.1-2.0 mm; width aperture 1.0-1.7 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–400 m. Degraded environments, agricultural land, urban areas, coastal areas. Introduced. Also in Brunei, Sarawak, Kalimantan. Distribution elsewhere: Pantropical. Natural range: Probably India, possibly Africa or the Mascarene islands.

Family **DYAKIIDAE** Gude & B B Woodward, 1921

Diagnosis for the Sabah species. Snails. Shell with up to 4–7 slowly to rapidly expanding whorls. Shell dextral or sinistral, small to large, wider than high; spire somewhat depressed conical to (inflated) lenticular; last whorl rounded to acutely keeled at the periphery. Teleoconch sculpture: Radial sculpture: Mainly growth lines in most species, or very fine, dense radial riblets in some; spiral sculpture absent or present, fine. Aperture without teeth. Peristome on the palatal side not thickened (but thickened in *Elaphroconcha*), not spreading. Umbilicus open, narrow (but closed in *Rhinocochlis chlorosoma*; rimate in some *Everettia*). Dimensions: Adults up to 7–21 mm high, 11.9–40 mm wide.

Animal. Mantle lobes absent.

Anatomy. Penial structure: Vas deferens attached distally to epiphallus. Epiphallus without flagellum. Dart sac with one or more apical glands.

Notes. On shell characters alone indistinguishable from Ariophantidae at family level; see notes under the diagnosis of the latter.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Shell sinistral. Periphery of outer whorl angular to acutely keeled
 - 2 Shell translucent. Radial sculpture of inconspicuous growth lines only above the periphery

Genus Rhinocochlis

- 2 –Shell opaque. Radial sculpture of fine riblets (which may have a granular crest because of intersecting spiral sculpture) above the periphery

 Genus *Dyakia*
- 1 Shell dextral. Periphery of outer whorl rounded
 - 3 Peristome with a thin, narrow lip on the inside of the palatal and the basal side Genus *Elaphroconcha*
 - 3 Peristome not thickened
 - 4 Shell up to 40 mm wide at c. 4 whorls, whorls rapidly expanding with the diameter of the second 7.8–8.5 mm Genus *Kalamantania*
 - 4 Shell up to 32 mm wide at c. 5 whorls or more, whorls slowly expanding with the diameter of the second whorl 2.3–5.5 mm (check also *Macrochlamys* and *Vitrinula* of Ariophantidae) Genus *Everettia*

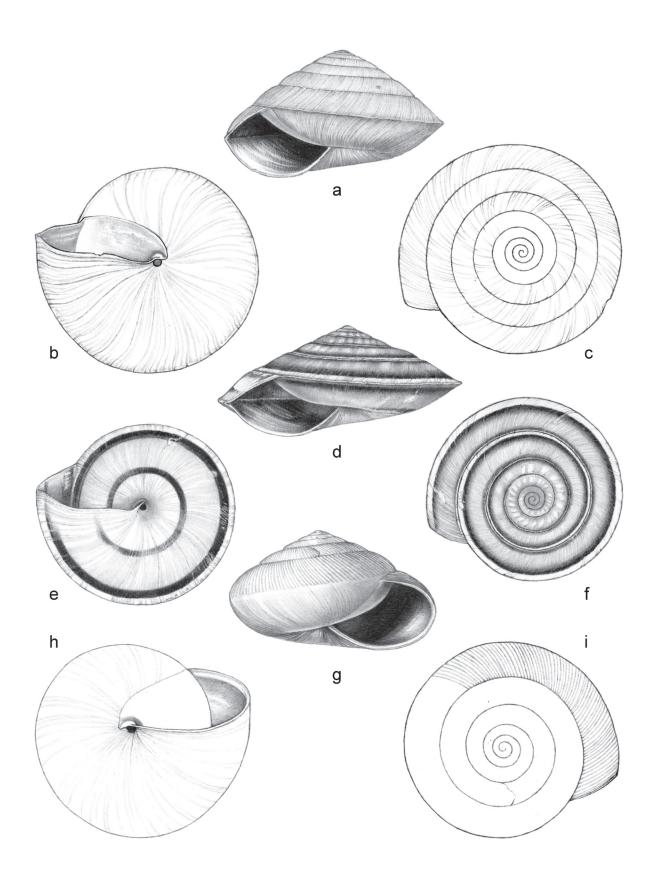


Fig. 132, a–c. *Dyakia hugonis* (L Pfeiffer, 1864), a. Frontal view, shell 21 mm high, b. Umbilical view, c. Apical view; d–f. *Dyakia regalis* (Benson, 1850), d. Frontal view, shell 17 mm high, e. Umbilical view, f. Apical view; g–i. *Elaphroconcha striata* (Gray, 1834), g. Frontal view, shell 14 mm high, h. Umbilical view, i. Apical view.



Fig. 133. Dyakia hugonis (L Pfeiffer, 1864).

Genus Dyakia Godwin-Austen, 1891

Diagnosis for the Sabah species. Shell sinistral, opaque. Periphery acutely keeled. Radial sculpture: Above the periphery fine riblets (which may have a granular crest because of intersecting spiral sculpture). Peristome not spreading and not thickened on the palatal and basal side, angular on the palatal side.

Dyakia hugonis (L Pfeiffer, 1864)

(fig. 132a–c, 133, map 28d)

Godwin-Austen 1891: 29; Smith 1894b: 454; Kobelt 1897: 54; Wiegmann 1898: 406; Von Martens 1908: 261; Laidlaw 1931: 191; 1963: 141; Saul 1967: 109; Maassen 2001: 105; Schilthuizen 2004: 94; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1; Uchida et al. 2013: 53, 54. – Helix hugonis Pfeiffer 1864 (1863): 523; 1866 (1866–1869): 304; 1868: 81; Kobelt 1881 (1880–1897): 605. – Nanina hugonis (L Pfeiffer) Von Martens 1867: 225; Issel 1874: 393; Tenison Woods 1888: 1024. – Nanina (Ariophanta) hugonis (L Pfeiffer) Pfeiffer & Clessin 1881: 55. – Type from Malaysia, 'Labuan island'.

Helix sinistra Bonnet 1864: 67. – Type from 'Borneo'.

Dyakia densestriata Schepman 1896: 154; Von Martens 1908: 261; Laidlaw 1963: 139; Solem 1964: 28; Schilthuizen & Rutjes 2001: 421. – *Nanina (Dyakia) densestriata* (Schepman) Von Martens 1908: 285. – Type from Indonesia, Kalimantan.

Description. Shell sinistral, large, thin, opaque, ochre-brown to dark brown, often paler brown towards the periphery. Surface approx. dull. Spire (low-)conical with slightly convex sides; apex hardly protruding, narrowly rounded. Whorls: Top whorls moderately convex, outer whorls somewhat less convex above the periphery, last whorl convex below, periphery pinched and acutely keeled. Sculpture. Protoconch with minute, dense, low radial riblets. Teleoconch. Radial sculpture: Growth lines, at uneven intervals raised or developing into fine, inconspicuous, low riblets. Next to this much finer, dense, wavy riblets are present. Spiral sculpture: Grooves, approx. as strong as the finest radial sculpture, which cut into the crests and create a granular surface visible at 20x magnifi-

cation. Aperture obliquely semi-elliptic, angular on the palatal side. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, shallow. Dimensions. Height up to 21 mm; width up to 35 mm; ratio height/width 0.5–0.6; diameter of the first three whorls 2.5–2.8 mm, 4.8–5.0 mm, 8.3–8.8 mm respectively; number of whorls up to c. 7; umbilicus c. 1 mm diam.; height aperture up to 12.5 mm; width aperture up to 21.0 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–1400 m. Primary and secondary forest on limestone and serpentinite bedrock. Distribution elsewhere: Malaysia (Peninsula) (see note), Indonesia (Natuna islands).

Notes. 1. The Peninsular Malaysia record (Laidlaw 1931: 191) may be based on misidentification; Laidlaw's description seems to apply to *Dyakia mackensiana* (Souleyet, 1841) rather than *D. hugonis*.

2. Extensive anatomical description in Wiegmann (1898).

Dyakia regalis (Benson, 1850)

(fig. 132d–f, map 28d)

Godwin-Austen 1891: 31; Von Martens 1908: 261. – *Helix regalis* Benson 1850b: 215; Reeve 1852 (1851–1854): Pl. 96, fig. 526; Pfeiffer 1853: 52; 1854 (1853–1860): 377; 1868: 82. – (?) *Ryssota regalis* (Benson) Wallace 1865: 407. – *Nanina regalis* (Benson) Von Martens 1867: 225; Tenison Woods 1888: 1024. – Type from Malaysia, 'Sarawak'.

Helix vittata A Adams & Reeve 1850 (1848–1850): 60; Metcalfe 1852 (1851): 70. – Type from Malaysia, Sabah, 'Balambangan'.

Dyakia regalis var. unicolor Godwin-Austen 1891: 31. – Type from 'NW Borneo'.

Dyakia duumvirorum Haas 1951: 624. – Type from Malaysia, Sarawak, near Kuching. [Not *Helix vittata* O F Müller].

Cross diagnosis. Differs from Dyakia hugonis by the undulating surface of (part of) the whorls, above the periphery.

Description. Shell sinistral, large, thin, opaque, entirely (ochre-)brown to dark brown(-purple), or the outer whorls with a sharply delineated white or pale yellow band below the suture, around the periphery and in the umbilical impression, the brown bands in between grading to black towards the white bands, or shell entirely white or yellowish. Surface somewhat shiny. Spire low-conical with slightly convex sides, apex somewhat protruding, narrowly rounded. Whorls: Top whorls moderately convex, outer whorls above the periphery somewhat less convex and (partly) with a gently undulating surface with undulations which fade out towards the suture and the periphery, last whorl convex below the periphery, periphery pinched and acutely keeled. Sculpture. Protoconch with minute, inconspicuous, low radial sculpture. Teleoconch. Radial sculpture: Growth lines, and at uneven intervals with rather densely placed but unevenly spaced, fine, low, narrow, rounded riblets. Spiral sculpture: Fine, shallow spiral grooves cutting into the crests of the riblets and dividing the riblets on the outer whorls into rows of minute granules, most distinctly so towards the periphery, spiral sculpture approx. absent in between the riblets. Aperture obliquely semi-elliptic, angular on the palatal side. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, shallow. Dimensions. Height up to 16 mm; width up to 34.5 mm; ratio height/width 0.45–0.55; diameter of the first three whorls 2.0–2.2 mm, 3.8–4.0 mm, 6.7–7.3 mm respectively; number of whorls up to c. 6; umbilicus c. 1 mm diam.; height aperture up to 11.0 mm; width aperture up to 19.0 mm.

Distribution in Sabah. Balambangan island only (old record). Elevation range: 0–100 m. Also in Sarawak, Kalimantan. Endemic to Borneo.

Note. The type of *Helix vittata* originates from Balambangan island, but we know no other records of this species from Sabah territory.

Genus *Elaphroconcha* Gude, 1911

(= Quantula H B Baker, 1941)

Diagnosis for the Sabah species. Shell dextral, opaque. Periphery rounded in adults. Radial sculpture: Above the periphery with fine, densely and slightly unevenly spaced riblets. Peristome not spreading, with a thin, narrow lip on the inside of the palatal and the basal side, rounded on the palatal side.

Elaphroconcha striata (Gray, 1834)

(fig. 132g–i, map 28e)

Nanina striata Gray 1834: 59; Von Martens 1867: 228; Issel 1874: 395. – Helix striata (Gray) Pfeiffer 1848a: 55. – Dyakia striata (Gray) Godwin-Austen 1891: 32. – Quantula striata (Gray) Van Benthem Jutting 1960: 17;

Maassen 2001: 107; Tan et al. 2012: 120; Phung et al. 2017: 84; Marzuki et al. 2021: 91. – Type of unknown origin.

Helix naninoides Benson 1842: 486; Reeve 1853 (1851–1854): Pl. 171, fig. 1158. – Nanina (Hemiplecta) naninoides (Benson) Pfeiffer 1855b: 121. – Nanina (Xesta) naninoides (Benson) Pfeiffer & Clessin 1881: 41. – Nanina naninoides (Benson) Tenison Woods 1881: 1017. – Syntypes from Singapore and 'Chusan'.

Cross diagnosis. Among dextral Sabah species with shells of similar shape identified by the fine and dense radial riblets above the periphery. From *Everettia* with a radial sculpture above the periphery it is identified by the somewhat thickened palatal peristome.

Description. Shell dextral, large, thin, opaque, ochre-brown above, pale yellow to pale brown below, sometimes with a narrow white peripheral band. Surface dull above, somewhat shiny below. Spire low-conical with slightly convex sides, apex narrowly rounded. Whorls: Top whorls moderately convex, outer whorls moderately convex above and below the periphery, periphery somewhat more narrowly rounded (angular in juveniles). Sculpture. Protoconch smooth, with minute, dense radial riblets just below the suture. Teleoconch. Radial sculpture: Above the periphery with fine, rather conspicuous, densely and slightly unevenly spaced, low, rounded riblets; below the periphery with raised growth lines only. Spiral sculpture: Above the periphery a few unevenly spaced, very shallow grooves, mainly cutting into the crests of the radial sculpture, approx. absent below the periphery. Next to this, shell surface minutely granulose (just visible at 40x magnification) below the periphery and in between the radial riblets above the periphery. Aperture crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere with a thin, narrow lip on the inside, not spreading. Umbilicus open, shallow. Dimensions. Height 12.0–17.5 mm; width 20.0–28.5 mm; ratio height/width 0.60–0.66; diameter of the first three whorls c. 2 mm, 4.0–4.3 mm, 7.0–8.0 mm respectively; number of whorls 5 3/8–6 1/4; umbilicus 0.8–1.0 mm diam.; height aperture 7.5–11.0 mm; width aperture 10.5–15 mm.

Distribution in Sabah. Labuan Marine Park only. Elevation range: 0–100 m. Secondary woodland, agricultural land, gardens; on various bedrock types. Also in Sarawak, Kalimantan. Distribution elsewhere: Laos, Malaysia (Peninsula), Singapore, Indonesia (Sumatra).

Genus *Everettia* Godwin-Austen, 1891 (By T-S Liew & J J Vermeulen)

Diagnosis for the Sabah species. Shell dextral, approx. translucent. Periphery rounded. Radial sculpture: Virtually absent, some growth lines only, or with fine riblets. Peristome not spreading and not thickened on the palatal and basal side, rounded on the palatal side. Shell up to 32 mm wide at c. 5 whorls or more, whorls slowly expanding with the diameter of the second whorl 2.3–5.0 mm.

Animal. Mantle lobes absent.

Anatomy. Penial structure: Vas deferens attached distally to epiphallus. Epiphallus without flagellum. Penis without caecum, retractor muscle laterally attached. Dart sac with apical glands, each with its own narrow duct to the dart sac. Dart present. Gametolytic sac directly opening into the vagina, without obvious gametolytic duct.

Notes. 1. Check also Vitrinula (Ariophantidae), with similar shells.

- 2. As a genus *Everettia* cannot be distinguished from *Macrochlamys* (Ariophantidae) on shell characters alone; see the notes under the generic diagnosis of *Macrochlamys*, and the notes under *Everettia jucunda* and *E. jucundior*, the two *Everettia* species most resembling a *Macrochlamys* species. Living specimens of *Everettia* are easily recognizable by the absence of appendages on the mantle edge; these are present in *Macrochlamys*. Further differences can be found in the genitalia, compare the diagnosis of both genera and fig. 93.
- 3. Several species on mount Tambuyukon and mount Kinabalu are strictly allopatric, see Liew et al. (2009: fig. 9) for distribution maps.
 - 4. For a molecular phylogeny and evolutionary history, see Liew et al. (2020).

KEY TO THE GROUPS

- 1 Last whorl above the periphery with dense radial riblets which are divided into rounded to distinctly elongated granules by spiral grooves which cut into their crests (check at 40x magnification)
 - 2 Last whorl above the periphery with granules which are approx. rounded in outline Group 1
 - 2 Last whorl above the periphery with granules which are distinctly elongated (at least three times as long as wide) in outline **Group 2**
- 1 Last whorl above the periphery without granules formed by intersecting radial and spiral sculpture
 - 3 Spiral sculpture present above the periphery of the outer whorl
 - 4 Spiral sculpture above the periphery of the outer whorl consisting of fine, widely and unevenly spaced, short, not entirely parallel threads (a few inconspicuous grooves may also be present) **Group 3**

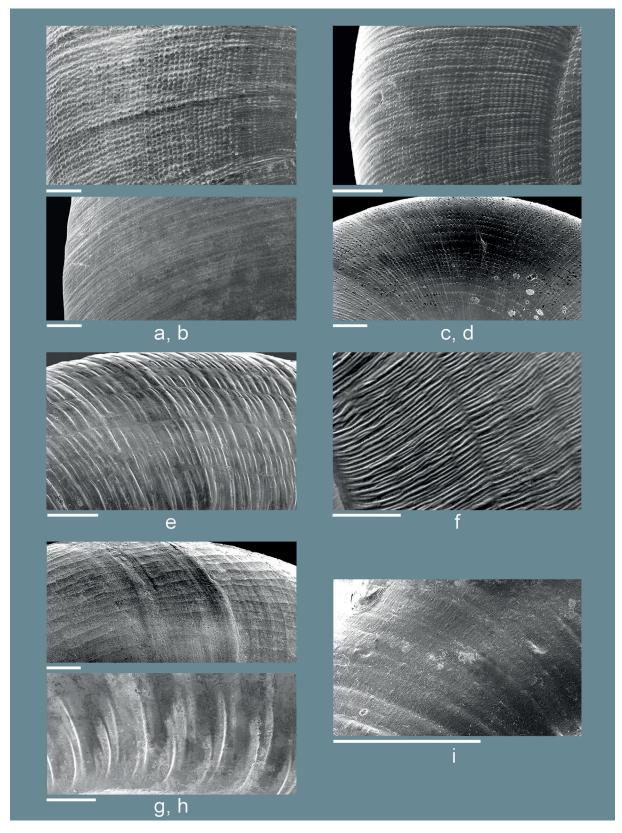


Fig. 134, a–b. *Everettia klemmantanica* Gude, 1918, a. Upper surface of ultimate whorl; b. lower surface of ultimate whorl; c–d. *Everettia jasilini* Liew, Schilthuizen & Vermeulen, 2009, c. Upper surface of ultimate whorl; d. lower surface of ultimate whorl; e. *Everettia corrugata williamsi* Liew, Schilthuizen & Vermeulen, 2009, upper surface of ultimate whorl; f. *Everettia paulbasintali* Liew, Schilthuizen & Vermeulen, 2009, upper surface of ultimate whorl; g–h. *Everettia corrugata corrugata* Laidlaw, 1937, g. Upper surface of ultimate whorl near the periphery; h. Upper surface of ultimate whorl near the suture; i. *Everettia safriei* Liew, Schilthuizen & Vermeulen, 2009 Upper surface of ultimate whorl.

- 4 Spiral sculpture above the periphery of the outer whorl consisting of approx. continuous grooves
 - 5 Spiral grooves above the periphery of the outer whorl widely spaced (c. 10 per mm) on the outer whorl (sometimes with much finer striation in between) **Group 4**
 - 5 Spiral grooves above the periphery of the outer whorl densely placed (40 or more per mm)

Group 5

- 3 Spiral sculpture absent above the periphery of the outer whorl
 - 6 Diameter of the fourth whorl 6.0–8.6 mm. Upper surface shell without conspicuous radial ribs

Group 6

6 – Diameter of the fourth whorl 8.0–14 mm; if diameter of fourth whorl 8.0–9.0 mm, then shell with distinct radial ribs above the periphery

Group 7

Group 1

Check also:

Everettia subconsul (Group 7). Some shells have a granulose sculpture above the periphery; this granulation, however, is much finer than in species of Group 1.

Everettia klemmantanica Gude, 1918

(fig. 134a-b, 136a-c, map 28f)

Gude 1918: 19; Liew et al. 2009: 531. - Type from 'Borneo'.

Cross diagnosis. In general shape resembling *Hemiplecta montivagans*, differs by the absence of oblique grooves and dents on the outer whorls, above the periphery.

Description. Shell large, thin, slightly translucent, pale green-corneous. Surface with a silky luster above the periphery, shiny below. Spire somewhat raised to depressed-conical with almost straight sides and a rounded apex. Whorls: Moderately convex above the periphery; last whorl distinctly convex below the periphery with the shell surface approx. parallel to the coiling axis just below the periphery; periphery slightly above half-way the height of the last whorl, obtusely angular. Sculpture. Protoconch smooth, with slight radial undulations, close to the teleoconch present only below the suture, spiral sculpture absent. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, above the periphery also with very fine, densely placed, sharply outlined riblets with a rounded crest. Spiral sculpture above the periphery increasingly conspicuous on the outer whorls, fine grooves approx. as densely placed as the radial riblets, deeply cutting into their crest and dividing them into rows of rounded granules; spiral striation absent below the periphery or locally present only, very dense (denser than above the periphery) and inconspicuous. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, partly covered by the columellar side of the peristome. Dimensions. Height up to 15.4 mm; width up to 30.8 mm; ratio height/width 0.49–0.50; diameter of the first four whorls 2.0–2.2 mm, 4.5–5.0 mm, 9.0–9.3 mm, c. 15 mm respectively; umbilicus up to 1 mm diam.; number of whorls up to 5 7/8; height aperture up to 11.8 mm; width aperture up to 16.0 mm.

Animal. Head, back, and tail grey, with a white median band. Sides white with grey stains in oblique stripes. Mantle reddish brown with white spots, last half whorl with transverse brown bands.

Distribution in Sabah. Rare in W: Mount Kinabalu, Crocker range. Elevation range: 500–2200 m. In primary forest, on sandstone/shale bedrock. Endemic to Sabah.

Note. A sample from Tawau Hills N.P. (sample JV 13195), has an evenly rounded periphery and spiral grooves which are more densely placed than the radial ribs they cross. It may represent a different species.

Everettia jasilini Liew, Schilthuizen & Vermeulen 2009

(fig. 134c–d, 136d–f, map 29a)

Liew et al. 2009: 538; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, Kinabalu N.P., NW part.

Cross diagnosis. Differs from *Everettia klemmantanica* by the less rapidly expanding whorls (diameter of the fourth whorl 8.2–11.5 mm, versus c. 15 mm), the evenly rounded periphery and the granular sculpture which extends on to the basal side of the shell.

Description. Shell medium-sized, thin, slightly translucent, yellow-corneous. Surface with a silky luster. Spire depressed-conical with slightly convex sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl equally convex below the periphery; periphery somewhat narrowly rounded. Sculpture. Protoconch with very fine, densely placed radial riblets, with more widely spaced, very fine spiral grooves cutting into their crest. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, above the periphery also with fine, rather densely placed, low, rather vaguely outlined riblets with a rounded crest. Spiral sculpture above the periphery: Rather densely and, particularly on the outer whorls, unevenly spaced rows of approx. circular, flattened

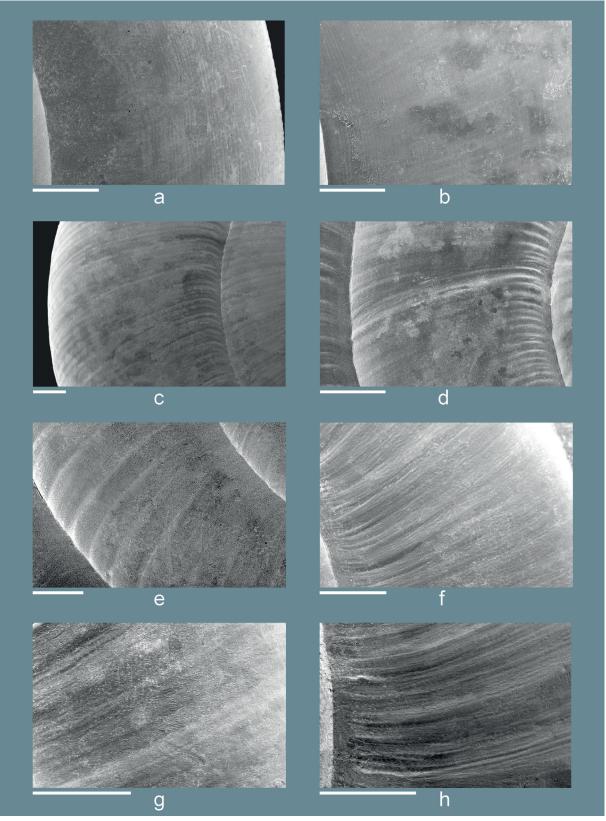


Fig. 135, a. *Everettia jucunda* (L Pfeiffer, 1864), upper surface of ultimate whorl; b. *Everettia jucundior* Liew, Schilthuizen & Vermeulen, 2009, upper surface of ultimate whorl; c. *Everettia dominiki* Liew, Schilthuizen & Vermeulen, 2009, upper surface of ultimate whorl; d. *Everettia layanglayang* Liew, Schilthuizen & Vermeulen, 2009, upper surface of penultimate whorl; e–h. *Everettia subconsul* (E A Smith, 1887); e. Form A, upper surface of penultimate whorl; f. Form B, upper surface of penultimate whorl; g. Form A, upper surface of penultimate whorl; h. Form C, upper surface of penultimate whorl. All scale bars are 0.5 mm.

granules on the crests of the radial riblets, on the outer whorl these rows become less distinct and more widely spaced towards the periphery but continue some distance below the periphery. Aperture broadly and somewhat obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, partly covered by the columellar side of the peristome. Dimensions. Height up to 8.8 mm; width up to 14.0 mm; ratio height/width 0.55–0.64; diameter of the first four whorls 1.2–1.8 mm, 2.5–3.8 mm, 4.8–6.5 mm, 8.2–11.5 mm respectively; umbilicus c. 0.5 mm diam.; number of whorls up to 4 7/8; height aperture up to 6.0 mm; width aperture up to 7.6 mm.

Animal. Head and back black. Mantle black with sparse, minute white spots.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2600–3500 m. In primary forest, on granodiorite bedrock. Endemic to Sabah.

Variability. Variable: In some shells the whorls expand more rapidly in width than in others.

Group 2

Check also:

Everettia subconsul (Group 7) may have a granulose sculpture above the periphery which, however, is much finer than in species of Group 2.

Everettia corrugata williamsi Liew, Schilthuizen & Vermeulen 2009 (fig. 134e, 136g–i, map 29b) Liew et al. 2009: 534; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, Gunung Kinabalu N.P.

Cross diagnosis. Differs from *Everettia paulbasintali* by the presence of a rather distinct, coarse undulation just below the suture of the outer whorls. Also, the radial sculpture is distinctly coarser. Also resembles *E. corrugata corrugata*, differs by the presence of spiral grooves above the periphery.

Description. Shell medium-sized, thin, somewhat translucent, green-corneous. Surface with a silky luster above the periphery, shiny below. Spire depressed-conical with almost straight sides and a rounded apex. Whorls: moderately convex above the periphery; last whorl moderately convex below the periphery; periphery approx. evenly rounded. Sculpture. Protoconch smooth, with slight radial undulations; spiral sculpture absent. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, above the periphery also with rather fine, densely placed, sharply outlined, wavy, riblets with a rounded crest; next to these rather distinct, coarse undulation just below the suture. Spiral sculpture above the periphery: Fine, widely spaced, very narrow grooves interrupting the radial riblets and dividing these into distinctly elongated sections; below the periphery locally traces of rather densely placed, rather fine, shallow grooves. Aperture broadly and slightly obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus rimate or open, narrow, partly covered by the columellar side of the peristome. Dimensions. Height up to 14.5 mm; width up to 18.8 mm; ratio height/width c. 0.64; diameter of the first four whorls c. 2.2 mm, 4.4 mm, 7.8 mm, 13.0 mm respectively; umbilicus up to 0.4 mm diam.; number of whorls up to 5.5/8; height aperture up to 8.8 mm; width aperture up to 11.5 mm.

Animal. Animal black or grey. Mantle dark, with sparse, white spots; on the last half whorl the spots are larger, interconnecting towards the edge.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2200–3200 m. In primary forest, on granodiorite and serpentinite bedrock. Endemic to Sabah.

Note. In the phylogeny of Liew et al. (2009: 546), *Everettia corrugata williamsi* is a paraphyletic grade to *E. corrugata corrugata* (Group 3). Our artificial grouping causes the two to come out in different groups.

Everettia paulbasintali Liew, Schilthuizen & Vermeulen 2009

(fig. 134f, 137a–f, map 28f)

Liew et al. 2009: 537. – Type from Malaysia, Sabah, Tawau Hills N.P. *Quantula* sp. Schilthuizen et al. 2003b: 42.

Description. Shell large, thin, opaque to somewhat translucent, green-corneous to brown-corneous. Surface with a silky luster above the periphery, shiny below. Spire moderately elevated to depressed-conical with almost straight sides and a rounded apex. Whorls: Moderately convex above the periphery; last whorl moderately convex below the periphery; periphery approx. evenly rounded. Sculpture. Protoconch smooth, with slight radial undulations; spiral sculpture absent. Teleoconch. Radial sculpture. Raised growth lines at uneven intervals, above the periphery also with very fine, very densely placed, sharply outlined, wavy, locally braided riblets with a rounded crest. Spiral sculpture above the periphery: Fine, widely spaced, very narrow grooves interrupting the radial riblets and dividing these into distinctly elongated sections; below the periphery (locally traces of) very densely placed, very fine, shallow grooves. Aperture broadly and slightly obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, slightly covered by the columellar side of the peristome or not. Dimen-

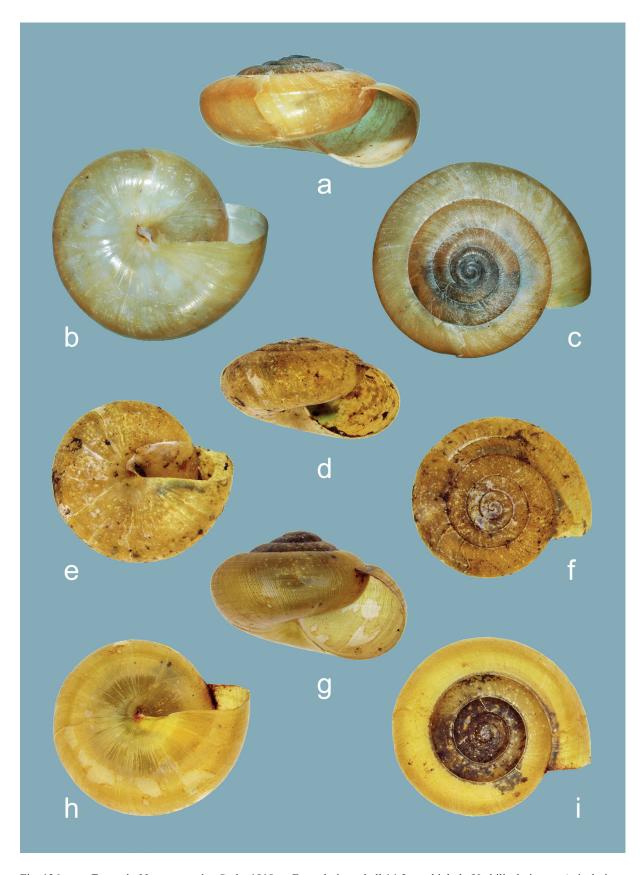


Fig. 136, a–c. *Everettia klemmantanica* Gude, 1918, a. Frontal view, shell 14.5 mm high, b. Umbilical view, c. Apical view; d–f. *Everettia jasilini* Liew, Schilthuizen & Vermeulen, 2009, d. Frontal view, shell 8.0 mm high, e. Umbilical view, f. Apical view; g–i. *Everettia corrugata williamsi* Liew, Schilthuizen & Vermeulen, 2009, g. Frontal view, shell 12.5 mm high, h. Umbilical view, i. Apical view.

sions. Height up to 19.8 mm; width up to 36.3 mm; ratio height/width 0.50–0.67; diameter of the first four whorls 1.5–2.1 mm, 3.0–4.2 mm, 5.6–7.2 mm, 9.8–11.5 mm respectively; umbilicus up to 1.5 mm diam.; number of whorls up to 6 3/8; height aperture up to 13.8 mm; width aperture up to 19.2 mm.

Animal. Head and back black, with a white median line. Sides stained black in oblique lines. Mantle with black markings, last half whorl with uneven transverse brown bands.

Distribution in Sabah. Rather common, but not in N and W. Elevation range: 0–800 m. In primary forest, on limestone, sandstone/shale and volcanic bedrock. Endemic to Sabah.

Group 3

Check also:

Everettia jucunda (Group 5). Shells may resemble *E. corrugata corrugata* (see below) but differ by the inconspicuous radial ribs just below the suture.

Everettia corrugata corrugata Laidlaw, 1937

(fig. 93b, 134g-h, 137g-i, 143a, map 29c)

Laidlaw 1937: 179; Tillier & Bouchet 1989 (1988): 287; Vermeulen 1996b: 285; Schileyko 2003: 1360; Liew et al. 2009: 531; Liew et al. 2010: Online Supporting Information, Appendix S1; Koene et al. 2013: 2. – Type from Malaysia, Sabah, mount Kinabalu.

Description. Shell medium-sized, thin, opaque or slightly translucent, green-corneous to brown-corneous. Surface shiny. Spire moderately elevated to depressed-conical with slightly convex sides and a rounded apex. Whorls: slightly to moderately convex above the periphery; last whorl equally convex below the periphery; periphery broadly rounded. Sculpture. Protoconch smooth but with crenulations below the suture. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, developing into rather coarse, moderately spaced, rather uneven, low, rather vaguely outlined riblets with a narrowly rounded crest, which are most conspicuous above the periphery and slowly fade out below, towards the umbilicus; next to these a coarser undulation is present above the periphery, which is most conspicuous just below the suture. Spiral sculpture above the periphery: Fine, widely and unevenly spaced, short, not entirely parallel threads which are most conspicuous in between the coarsest radial riblets, and which are virtually absent in some shells, and which may occur next to scattered, shallow grooves in others; below the periphery similar, if sometimes slightly more distinct and continuous threads, next to this coarser but inconspicuous, widely spaced, low, vaguely outlined spiral threads may occur. Aperture broadly and somewhat obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus rimate or open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 11.9 mm; width up to 19.6 mm; ratio height/width 0.59-0.65; diameter of the first four whorls 2.3-2.5 mm, 4.8-5.2 mm, 8.5-8.7 mm, 11.5-15.0 mm respectively; umbilicus up to c. 0.5 mm diam.; number of whorls up to 5 1/8; height aperture up to 8.0 mm; width aperture up to 10.2 mm.

Animal. Animal black or grey, sometimes with a vaguely outlined grey median line. Mantle dark, with sparse, white spots; on the last half whorl the spots are larger and interconnecting towards the edge.

Distribution in Sabah. Highlands: Kinabalu only. Elevation range: 2500–3500 m. In primary forest, on gran-odiorite and serpentinite bedrock. Endemic to Sabah.

Note. For subsp. williamsi: see Group 2.

Everettia safriei Liew, Schilthuizen & Vermeulen 2009

(fig. 134i, 138a–c, map 29d)

Liew et al. 2009: 540; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, Gunung Kinabalu N.P., S part.

Cross diagnosis. Differs from *Everettia corrugata corrugata* by the absence of coarse radial undulations just below the suture, and by the much finer radial sculpture above the periphery. Also, the whorls are somewhat less rapidly expanding (diameter of the fourth whorl c. 9 mm, versus 11.5–15 mm).

Description. Shell small to medium-sized, thin, slightly translucent, green-corneous to brown-corneous. Surface with a silky luster above the periphery, shiny below. Spire moderately elevated with somewhat convex sides and a widely rounded apex. Whorls: Moderately convex above the periphery; last whorl convex below the periphery; periphery evenly rounded. Sculpture. Protoconch smooth, or with inconspicuous, densely placed, spiral grooves. Teleoconch. Radial sculpture: Above the periphery with rather fine, moderately and unevenly spaced, low, rather vaguely outlined riblets with a rounded crest, which fade out on the basal side of the shell, towards the umbilicus. Spiral sculpture above the periphery consisting of very fine (just visible at 40x magnification), dense, unevenly spaced, short, not entirely parallel, often somewhat braided threads, spiral sculpture absent below the periphery. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 6.3 mm; width up

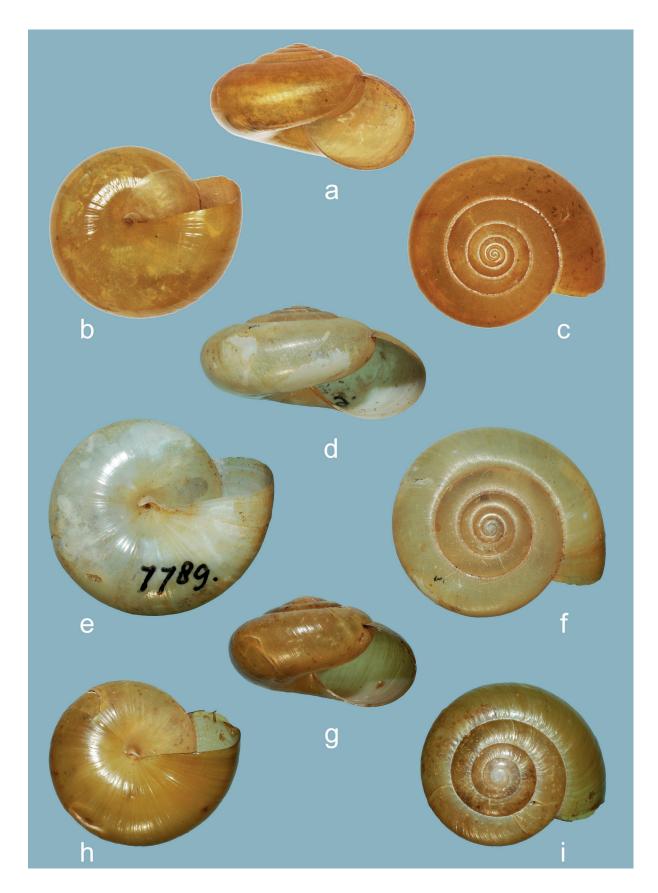


Fig. 137, a–f. *Everettia paulbasintali* Liew, Schilthuizen & Vermeulen, 2009, a. Frontal view, shell 11.5 mm high, b. Umbilical view, c. Apical view, d. Frontal view, shell 11.0 mm high, e. Umbilical view, f. Apical view; g–i. *Everettia corrugata corrugata* Laidlaw, 1937, g. Frontal view, shell 10.5 mm high, h. Umbilical view, i. Apical view.

to 10.5 mm; ratio height/width c. 0.68; diameter of the first four whorls c. 1.4 mm, 3.0 mm, 5.4 mm, 9.0 mm respectively; umbilicus c. 0.3 mm diam.; number of whorls up to 5 1/8; height aperture up to 4.0 mm; width aperture up to 5.4 mm.

Animal. Head and back uniformly black. Mantle brownish, last half whorl with sparse, uneven black and white markings.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2200–3500 m. In primary forest, on serpentinite and granodiorite bedrock. Endemic to Sabah.

Group 4

Everettia interior Liew, Schilthuizen & Vermeulen 2009

(fig. 138d-f, 143b, map 28f)

Liew et al. 2009: 536. - Type from Malaysia, Sabah, Sapulut area, Gua Sanaron.

Description. Shell medium-sized to large, thin, slightly translucent, pale yellow-corneous to pale green-corneous. Surface shiny. Spire slightly raised to depressed-conical, with almost straight sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl slightly to moderately convex below the periphery; periphery slightly narrowly rounded. Sculpture. Protoconch smooth, with slight radial undulations below the suture; spiral sculpture absent. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, in some shells locally developing into fine, rather densely placed, somewhat uneven, low riblets with a narrowly rounded crest. Spiral sculpture above the periphery increasingly conspicuous on the outer whorls, consisting of fine, widely spaced (c. 10 per mm on the last whorl), continuous, shallow grooves, with or without a much finer striation in between; below the periphery the grooves are densely placed. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, not or hardly covered by the columellar side of the peristome. Dimensions. Height up to 11.2 mm; width up to 20.0 mm; ratio height/width c. 0.53–0.56; diameter of the first four whorls 1.8–2.3 mm, 3.3–4.4 mm, 6.0–7.8 mm, 10.0–14.0 mm respectively; umbilicus up to 0.8 mm diam.; number of whorls up to 5 3/8; height aperture up to 8.2 mm; width aperture up to 9.5 mm.

Animal. Head, back and tail black with a white median line. Mantle black with crowded white spots, approx. arranged in transverse markings on the last half-whorl.

Distribution in Sabah. Sinobang and Sapulut only. Elevation range: 300–500 m. In primary forest and secondary forest, on limestone bedrock. Endemic to Sabah.

Everettia lapidini Liew, Schilthuizen & Vermeulen 2009

(fig. 138g-i, map 29e)

Liew et al. 2009: 536. – Type from Sabah, Kinabalu N.P., S part.

Cross diagnosis. Differs from *Everettia interior* by the less rapidly expanding whorls (diameter of the fourth whorl 8.3–8.5 mm, versus 10.0–14.0 mm).

Description. Shell large, thin, slightly translucent, pale yellow-corneous to green-corneous to pale brown-corneous. Surface with a silky luster above the periphery, shiny below. Spire somewhat raised with almost straight sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl slightly to moderately convex below the periphery; periphery approx. evenly rounded in fully adult shells, in juveniles narrowly rounded to obtusely angular slightly above half-way the height of the last whorl. Sculpture. Protoconch smooth, with slight radial undulations particularly below the suture; spiral sculpture absent. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, developing into rather fine, rather densely placed, rather uneven, low riblets with a narrowly rounded crest, which are most conspicuous just below the suture, then merge a few together to larger but lower riblets which slowly fade out below the periphery. Spiral sculpture above the periphery increasingly conspicuous on the outer whorls, consisting of fine, widely spaced (c. 10 per mm on the last whorl), continuous, shallow grooves; below the periphery the grooves are somewhat less conspicuous and more densely placed. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus rimate or open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 17.1 mm; width up to 31.5 mm; ratio height/width c. 0.54; diameter of the first four whorls 1.5-1.7 mm, 2.8-3.0 mm, 5.0-5.2 mm, 8.3-8.5 mm respectively; umbilicus up to 0.5 mm diam.; number of whorls up to 5 5/8; height aperture up to 12.7 mm; width aperture up to 17.3 mm.

Animal. Head and back black, tail mottled black. Mantle black with sparse, tiny white spots, last half whorl with evenly spaced, transverse black markings near the shell suture.

Distribution in Sabah. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 1300–2300 m. In primary forest, on limestone, sandstone/shale and serpentinite bedrock. Endemic to Sabah.

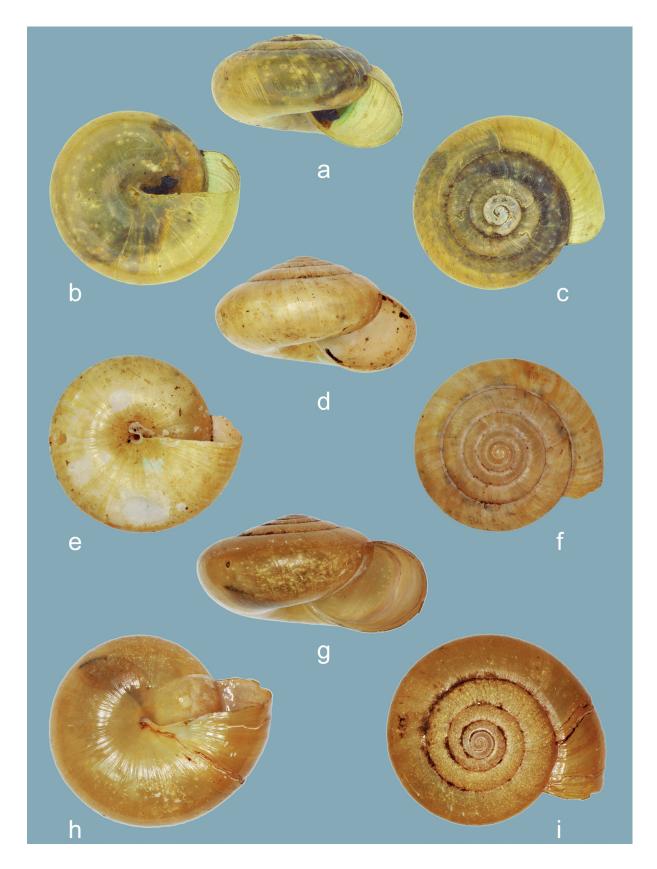


Fig. 138, a–c. *Everettia safriei* Liew, Schilthuizen & Vermeulen, 2009, a. Frontal view, shell 6.4 mm high, b. Umbilical view, c. Apical view; d–f. *Everettia interior* Liew, Schilthuizen & Vermeulen, 2009, d. Frontal view, shell 10.0 mm high, e. Umbilical view, f. Apical view; g–i. *Everettia lapidini* Liew, Schilthuizen & Vermeulen, 2009, g. Frontal view, shell 17.0 mm high, h. Umbilical view, i. Apical view.

Group 5

Everettia jucunda (L Pfeiffer, 1864)

(fig. 135a, 139a–c, 143c, map 29e)

Godwin-Austen 1891: 34; Smith 1895: 107; Kobelt 1897: 50; Wiegmann 1898: 352; Von Martens 1908: 260; Schileyko 2003: 1360; Liew et al. 2009: 520; Phung et al. 2017: 82. – *Helix jucunda* Pfeiffer 1864 (1863): 524; 1866 (1866–1869): 307; 1868: 101. – *Nanina jucunda* (Pfeiffer) Von Martens 1867: 240; Issel 1874: 398; Tenison Woods 1888: 1018. – *Nanina (Macrochlamys) jucunda* (Pfeiffer) Pfeiffer & Clessin 1881: 43. – *Macrochlamys (Everettia) jucunda* (Pfeiffer) Kobelt 1901 (1898–1905): 1014. – Type from Malaysia, 'Labuan island'

Cross diagnosis. Characterized by the outer whorls which more slowly expand in width then in other Everettia of similar size, in particular E. jucundior: A fully grown, c. 22 mm wide shell of E. jucunda has c. 6 3/4 whorls, a shell of the same size of E. jucundior c. 5 1/2. Also, E. jucundior has more distinct and more continuous spiral sculpture on the last whorl, above the periphery. The slowly expanding outer whorls also distinguishes E. jucunda from Macrochlamys indica (Ariophantidae); see the cross diagnosis with that species.

Description. Shell medium-sized to large, thin, slightly translucent, (pale) yellow-corneous to (pale) brown-corneous. Surface shiny. Spire moderately raised to depressed-conical, with almost flat to convex sides and a rounded apex. Whorls: moderately convex above the periphery; last whorl moderately convex below the periphery; periphery evenly rounded. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, in some shells locally developing into fine, rather densely placed, somewhat uneven, low riblets with a narrowly rounded crest. Spiral sculpture consisting of inconspicuous, very fine, very dense (c. 40 per mm on the last whorl), shallow grooves which usually are only locally present. Aperture broadly and slightly obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 12.0 mm; width up to 22.0 mm; ratio height/width 0.50–0.64; diameter of the first four whorls 1.5–1.8 mm, 3.1–3.6 mm, 5.0–6.2 mm, 8.0–10.5 mm respectively; umbilicus up to 0.8 mm diam.; number of whorls up to 6 3/4; height aperture up to 9.5 mm; width aperture up to 11.6 mm.

Animal. Head and back black with a wide, white median band. Tail with greyish bands on either side of the median line. Sides without markings. Mantle covered with brown, uneven markings, last half whorl with evenly spaced darker brown transverse bands.

Distribution in Sabah. Locally common in W: Labuan Marine Park, Klias peninsula, Pulau Tiga Park. Elevation range: 0–100 m. Primary forest, secondary woodland, coastal woodland, on limestone and sandstone/shale bedrock. Also in Brunei, Sarawak. Endemic to Borneo.

Everettia jucundior Liew, Schilthuizen & Vermeulen 2009

(fig. 135b, 139d–f, 143d, map 29e)

Liew et al. 2009: 538. – Type from Malaysia, Sabah, Tawau Hills N.P.

Everettia subconsul auct. Laidlaw 1931: 196.

[Not Everettia subconsul E A Smith].

Cross diagnosis. Differs from *Macrochlamys indica* (Ariophantidae) by the rather distinct, continuous spiral sculpture on the last whorl, above the periphery. Also, the last whorl is less distinctly convex above and below the periphery, and the periphery itself is more narrowly rounded.

Description. Shell large, thin, slightly translucent, pale green-corneous to pale brown-corneous. Surface silky above, shiny below. Spire moderately raised to depressed-conical, with almost straight sides and a rounded apex. Whorls: Moderately convex above the periphery; last whorl moderately convex below the periphery; periphery somewhat narrowly rounded. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, in some shells locally developing into fine, rather densely placed, somewhat uneven, low riblets with a narrowly rounded crest. Spiral sculpture above the periphery consisting of fine, very dense (c. 40 or more per mm on the last whorl), continuous, shallow grooves; below the periphery similar grooves, but often somewhat less conspicuous. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus closed to open, narrow, partly covered by the columellar side of the peristome. Dimensions. Height up to 11.8 mm; width up to 22.0 mm; ratio height/width 0.52–0.61; diameter of the first four whorls 1.3–1.5 mm, 3.0–3.3 mm, 5.5–6.0 mm, 8.0–10.2 mm respectively; umbilicus up to 1.0 mm diam.; number of whorls up to 5 1/2; height aperture up to 9.0 mm; width aperture up to 11.8 mm.

Animal. Head and back black with a wide, white median band. Tail with greyish bands on either side of the median line. Sides without markings. Mantle black with crowded tiny white spots and evenly spaced transverse black bands in the last half whorl.

Distribution in Sabah. Scattered localities in E; elsewhere in Sinobang only. Elevation range: 0-800 m. In

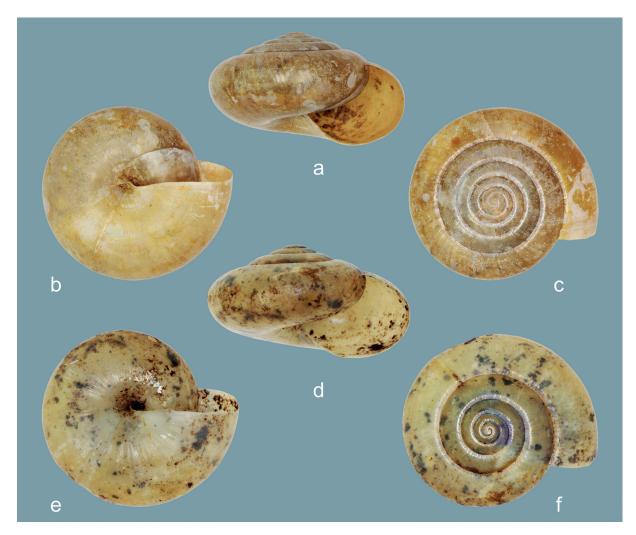


Fig. 139, a–c. *Everettia jucunda* (L Pfeiffer, 1864), a. Frontal view, shell 11.5 mm high, b. Umbilical view, c. Apical view; d–f. *Everettia jucundior* Liew, Schilthuizen & Vermeulen, 2009, d. Frontal view, shell 11.0 mm high, e. Umbilical view, f. Apical view.

primary forest and secondary forest, on limestone bedrock. Endemic to Sabah.

Group 6

Everettia monticola Liew, Schilthuizen & Vermeulen 2009 (fig. 140a–c, 143e, map 29f) Liew et al. 2009: 541. – Type from Malaysia, Sabah, Gunung Kinabalu N.P., S part.

Description. Shell small to medium-sized, thin, slightly translucent, pale green-corneous. Surface shiny. Spire somewhat raised with almost straight sides and a rounded apex. Whorls: Moderately convex above the periphery; last whorl moderately convex below the periphery; periphery evenly rounded. Sculpture. Protoconch smooth, with slight radial undulations particularly below the suture; spiral sculpture absent. Teleoconch. Radial sculpture: With or without few raised growth lines at somewhat uneven intervals, in some shells developing into rather fine, rather densely placed, rather uneven, low riblets just below the suture. Spiral sculpture absent above the periphery, below the periphery locally traces of very fine, densely placed, shallow grooves. Aperture obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 7.0 mm; width up to 11.9 mm; ratio height/width 0.53–0.60; diameter of the first four whorls 1.2–1.4 mm, 2.3–2.6 mm, 4.2–4.5 mm, 7.0–7.5 mm respectively; number of whorls up to 5 1/8; height aperture up to 5.4 mm; width aperture up to 6.5 mm.

Animal. Head and back dark, with a pale median line. Sides pale with dark staining. Mantle dark with large white spots.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 900–3000 m. In damp primary forest, on limestone and sandstone/shale bedrock. Endemic to Sabah.

Everettia planispira Liew, Schilthuizen & Vermeulen 2009

(fig. 140d–f, 143f, map 30a)

Liew et al. 2009: 541. – Type from Malaysia, Sabah, Beluran district. Ulu Tungud F.R.

Cross diagnosis. Differs from Everettia monticola by the approx. flat spire.

Description. Shell small to medium-sized, thin, slightly translucent, pale green-corneous. Surface shiny. Spire not or hardly raised with almost straight sides and a rounded apex. Whorls: Moderately convex above the periphery; last whorl moderately convex below the periphery; periphery evenly rounded. Sculpture. Protoconch smooth, with slight radial undulations particularly below the suture; spiral sculpture absent. Teleoconch. Radial sculpture; With or without few raised growth lines at somewhat uneven intervals. Spiral sculpture absent above the periphery, below the periphery in some shells locally traces of very fine, densely placed, shallow grooves. Aperture obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus closed, or open, narrow, largely covered by the columellar side of the peristome. Dimensions. Height up to 7.3 mm; width up to 13.4 mm; ratio height/width 0.48–0.58; diameter of the first four whorls 1.1–1.3 mm, 2.0–2.5 mm, 3.8–4.5 mm, 6.0–8.6 mm respectively; number of whorls up to 5 3/8; height aperture up to 5.8 mm; width aperture up to 6.9 mm.

Distribution in Sabah. Widespread and rather common, but not in SW. Elevation range: 0–700 m. In primary and secondary forest, on limestone and sandstone/shale bedrock. Endemic to Sabah.

Group 7

Check also:

Everettia jucunda (Group 5). Shells virtually without spiral sculpture differ from species in Group 7, and particularly from E. subconsul form A. by the narrower outer whorl (see note under E. jucunda).

Everettia corrugata corrugata (Group 3). Shells without spiral sculpture above the periphery differ from species of Group 7 by the coarse radial ribs just below the suture. In this character, these may resemble *E. dominiki*, but differ by the more rapidly expanding whorls (diameter of the fourth whorl 11.5–15.0 mm, versus 8.2–8.8 mm).

Everettia dominiki Liew, Schilthuizen & Vermeulen 2009 (fig. 135c, 141a–c, 144a, map 30b) Liew et al. 2009: 542. – Type from Malaysia, Sabah, Kinabalu N.P. NE part.

Cross diagnosis. Differs from *Everettia layanglayang* and *E. subconsul* by the shiny, evenly ribbed upper surface of the shell. Also, the whorls expand less rapidly (fourth whorl 8.2–8.8 mm diam, versus 9–14 mm).

Description. Shell medium-sized, thin, slightly translucent, green-corneous. Surface shiny. Spire depressed-conical with slightly convex sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl equally convex below the periphery; periphery broadly rounded. Sculpture. Protoconch smooth but with crenulations below the suture. Teleoconch. Radial sculpture: Raised growth lines at uneven intervals, above the periphery also with rather fine to rather coarse, moderately and approx. evenly spaced, rather vaguely outlined riblets with a rounded crest, which are most conspicuously present just below the suture, and may be rather inconspicuous elsewhere. Spiral sculpture absent above the periphery; below the periphery densely placed, shallow, approx. continuous grooves. Aperture broadly and somewhat obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, partly covered by the columellar side of the peristome. Dimensions. Height up to 8.8 mm; width up to 13.6 mm; ratio height/width 0.51–0.60; diameter of the first four whorls 1.2–1.6 mm, 2.7–2.9 mm, 4.8–6.1 mm, 8.2–8.8 mm respectively; umbilicus up to 0.5 mm diam.; number of whorls up to 5 1/4; height aperture up to 6.0 mm; width aperture up to 7.5 mm.

Animal. Head and back black. Sides greyish. Mantle brownish, with small dark spots and larger white spots. *Distribution in Sabah*. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 1500–3200 m. In primary forest, on sandstone/shale, granodiorite and serpentinite bedrock. Endemic to Sabah.

Everettia layanglayang Liew, Schilthuizen & Vermeulen 2009 (fig. 135d, 141d–i, 143g, map 30c) Liew et al. 2009: 534. – Type from Malaysia, Sabah, Kinabalu N.P., S part.

Cross diagnosis. Resembles very much *Everettia subconsul*, particularly form a. It differs by the color of the animal, particularly of the mantle: Approx. black, with sparse, small pale spots, which may become slightly larger and more numerous towards the mantle edge (versus mantle ochre-brown, last half-whorl with narrow transverse black markings at approx. regular intervals). Also, the radial riblets on the shell above the periphery, and particu-



Fig. 140, a–c. *Everettia monticola* Liew, Schilthuizen & Vermeulen, 2009, a. Frontal view, shell 7.0 mm high, b. Umbilical view, c. Apical view; d–f. *Everettia planispira* Liew, Schilthuizen & Vermeulen, 2009, d. Frontal view, shell 7.0 mm high, e. Umbilical view, f. Apical view.

larly just below the suture, is more distinct, and rougher (but not as evenly ribbed as in E. dominiki).

Description. Shell medium-sized, thin, slightly translucent, yellow-corneous to green-corneous to brown-corneous. Surface with a silky luster above the periphery, shiny below. Spire moderately elevated with almost straight sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl convex below the periphery; periphery approx. evenly rounded. Sculpture. Protoconch smooth, with slight radial undulations; spiral sculpture absent. Teleoconch. Radial sculpture: Above the periphery with rather fine, moderately and unevenly spaced, even or uneven, low, rather vaguely outlined riblets with a rounded crest, which are most conspicuously present just below the suture, and which fade out further down, or on the basal side of the shell, towards the umbilicus. Spiral sculpture absent above the periphery, below the periphery consisting of fine, moderately spaced, continuous, shallow grooves. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, half-covered by the columellar side of the peristome. Dimensions. Height up to 11.5 mm; width up to 20 mm; ratio height/width 0.55–0.58; diameter of the first four whorls 1.8–2.0 mm, 4.0–4.2 mm, 7.0–7.2 mm, 11.8–12.5 mm respectively; umbilicus up to 0.6 mm diam.; number of whorls up to 5 1/8; height aperture up to 8.8 mm; width aperture up to 10.0 mm.

Animal. Head and back uniformly pink to red-brown to black. Mantle approx. black, with sparse, small, pale spots, which may become slightly larger and more numerous towards the mantle edge.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 1100–3300 m. Primary forest, on sandstone/shale and serpentinite bedrock. Endemic to Sabah.

Everettia subconsul (E A Smith, 1887)

(fig. 135e-h, 142a-i, 143h, map 30d)

Godwin-Austen 1891: 35, sub *E. aglaia*; Smith 1895: 100, 107; Von Martens 1908: 260; Laidlaw 1931: 196; 1937: 180; Vermeulen 1996b: 285; Liew et al. 2009: 522; Liew et al. 2010: Online Supporting Information, Appendix S1; Uchida et al. 2013: 53, 54; Phung et al. 2017: 83. – *Nanina subconsul* Smith 1887a: 132. – *Macrochlamys subconsul* (E A Smith) Smith 1887b: 217. – *Macrochlamys (Everettia) subconsul* (E A Smith) Kobelt 1901 (1898–1905): 1011. – *Quantula subconsul* (E A Smith) Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41. – Type from 'North Borneo'.

Everettia bangueyensis Smith 1895: 100, 108; Von Martens 1908: 260. – Macrochlamys (Everettia) bangueyensis (E A Smith) Kobelt 1901 (1898–1905): 1013. – Type from Malaysia, Sabah, 'Banguey Island'.

Xesta themis Smith 1895: 100. – Nanina (Xestina) themis (E A Smith) Kobelt 1901 (1898–1905): 994. – Xestina themis (E A Smith) Von Martens 1908: 260; Haas 1951: 623. – Quantula themis (E A Smith) Solem 1964: 29. – Everettia themis (E A Smith) Liew et al. 2009: 526. – Type from Malaysia, Sabah, 'Upper Padas' river.

Everettia occidentalis Liew et al. 2009: 540. – Type from Malaysia, Sabah, Ulu Padas.

Everettia consul auct. Smith 1895: 107. - Nanina consul auct. Issel 1874: 398 (Labuan records only).

Everettia 'spec. large' Schilthuizen et al. 2003b: 42.

Everettia 'unidentified' Schilthuizen 2004: 94.

Everettia 'sp. 4' Schilthuizen et al. 2011: 4.

Everettia sp. Foon et al. 2018: 96.

[Not *Everettia subconsul* auct. Laidlaw 1931: 196; = *Everettia jucundior* Liew, Schilthuizen & Vermeulen]. [Not *Helix consul* L Pfeiffer].

Cross diagnosis. Everettia klemmantanica (Group 1) and *E. paulbasintali* (Group 2) have similar markings on the last half-whorl of the mantle; they differ by the coarse sculpture on the shell, above the periphery.

Description. Shell medium-sized to large, thin, opaque to slightly translucent, (pale) green-corneous, yellow-corneous to brown-corneous. Surface almost dull to shiny above the periphery, shiny below. Spire moderately elevated with almost straight sides and a rounded apex. Whorls: Slightly convex above the periphery; last whorl convex below the periphery; periphery approx. evenly rounded or obtusely angular, slightly above half-way the height of the last whorl. Sculpture. Protoconch smooth, or with radial undulations; spiral sculpture absent. Teleoconch. Radial sculpture: Above the periphery with (a few) raised growth lines, in some shells locally developing into rather fine, moderately and unevenly spaced, low, rather vaguely outlined riblets with a rounded crest, which fade out on the basal side of the shell, towards the umbilicus; next to this a much finer, approx. oblique pattern of wavy, partly braided ridges with or without a minutely granulose crest (just visible at 40x magnification) may also be present over the entire upper surface or in patches. Spiral sculpture absent above the periphery, below the periphery absent or consisting of fine, moderately spaced, continuous, shallow grooves. Aperture broadly and obliquely crescent-shaped, peristome neither widened, nor thickened. Umbilicus open, narrow, up to half-covered by the columellar side of the peristome. Dimensions. Height up to 18.5 mm; width up to 34 mm; ratio height/ width 0.52–0.58; diameter of the first four whorls 1.5–2.0 mm, 3.0–4.0 mm, 5.2–7.2 mm, 9.0–14 mm respectively; umbilicus up to c. 2.0 mm diam.; number of whorls up to 6 3/4; height aperture up to 13.2 mm; width aperture up to 17 mm.

Animal. Head and back black, with or without a white or pink median line. Sides pink, stained black in oblique lines. Mantle ochre-brown, last half-whorl with narrow transverse black markings at approx. regular intervals.

Distribution in Sabah. Widespread, common. Elevation range: 0–1900 m. In primary forest, coastal forest, also in secondary woodland, on limestone, sandstone/shale, and serpentinite bedrock. Endemic to Sabah.

Variability. Several localized forms of rather different appearance can be distinguished:

Form A (fig. 135e, g, 142a–c). Shell medium-sized, (pale) green-corneous. Periphery of last whorl usually rounded. Teleoconch above the periphery often with inconspicuous radial sculpture; microsculpture absent or only locally present, very inconspicuous. Dimensions. Height up to 11.5 mm; width up to 21 mm; number of whorls up to 5 1/2; diameter of the fourth whorl 9.0–14.0 mm.

Distribution in Sabah. Widespread and common in N and W; elsewhere in Sinobang, Sapulut, lower Kinabatangan. Elevation range: 0–1900 m.

May resemble *Everettia interior* and *E. jucundior*; differs by the absence of spiral sculpture above the periphery. Material from higher altitudes usually have a relatively thin, translucent shell. Includes the types of *Nanina subconsul* and *Everettia occidentalis*.

Form B (fig. 135f, 142d–f). Shell large, pale green-corneous. Periphery of last whorl rounded or slightly and obtusely angular slightly above half-way the height of the last whorl. Teleoconch above the periphery with rather fine, low, rather vaguely outlined radial riblets with a rounded crest; microsculpture of wavy, partly braided ridges usually present locally. Dimensions. Height up to 18.5 mm; width up to 34 mm; number of whorls up to 6 3/4;

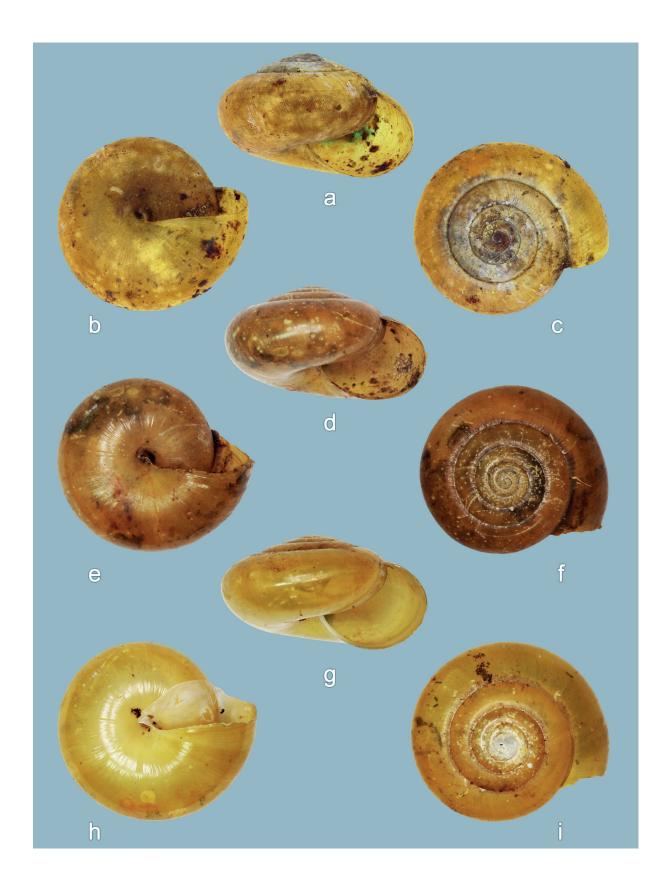


Fig. 141, a–c. *Everettia dominiki* Liew, Schilthuizen & Vermeulen, 2009, a. Frontal view, shell 8.5 mm high, b. Umbilical view, c. Apical view; d–i. *Everettia layanglayang* Liew, Schilthuizen & Vermeulen, 2009, d. Frontal view, shell 10.0 mm high, e. Umbilical view, f. Apical view, g. Frontal view, shell 10.5 mm high, h. Umbilical view, i. Apical view.

diameter of the fourth whorl 9.5–11.0 mm.

Distribution in Sabah. Widespread and common in the central part and E. Elevation range: 0-500 m.

May resemble *Everettia klemmantanica* and *E. paulbasintali* in general appearance; differs by the much finer and more inconspicuous granular sculpture.

Form C (fig. 135h, 142g–i). Shell medium-sized, yellow-corneous to brown-corneous. Periphery of last whorl obtusely angular slightly above half-way the height of the last whorl. Teleoconch above the periphery with rather distinct radial riblets with a rounded crest; microsculpture of wavy, partly braided ridges present over most of the upper surface, giving it a dull appearance. Dimensions. Height up to 11 mm; width up to 20 mm; number of whorls up to 5 1/2; diameter of the fourth whorl 11.5–13.5 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range; in N on Balambangan island. Elevation range: 0–1400 m.

Shares the obtusely angular periphery with *Everettia klemmantanica*; differs by the smaller size but somewhat more rapidly expanding whorls (fourth whorl 11.5–13.2 mm diam., versus 9.5–11.0 mm) and the finer microsculpture above the periphery. Includes the type of *Xesta themis*.

Genus Kalamantania Laidlaw, 1931

Diagnosis for the Sabah species. Shell dextral, translucent. Periphery slightly and obtusely angular. Radial sculpture: Growth lines, at uneven intervals raised or developing into slight, inconspicuous, low riblets. Peristome not spreading and not thickened on the palatal and basal side, rounded on the palatal side. Shell up to 40 mm wide at c. 4 whorls, whorls rather rapidly expanding, diameter of the second 7.8–8.5 mm.

Kalamantania whiteheadi (Godwin-Austen, 1891)

(fig. 144b-e, map 30e)

Laidlaw 1931: 194; 1937: 180; Vermeulen 1996b: 286; Schilthuizen 2004: 95; Clements et al. 2008: 2761; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Helicarion whiteheadi* Godwin-Austen 1891: 24; Von Martens 1908: 259. – Type from Malaysia, Sabah, 'Kina Balu'.

Helicarion rugosa Fulton 1905: 91; Saul 1967: 109. – Type from 'N. Borneo'.

Cross diagnosis. Differs from other species with a shell with a few, rapidly expanding whorls (such as *Helicarion*) by the larger size of the shell and the rough sculpture on its upper surface.

Description. Shell dextral, large, thin, opaque, olive-green to brown, sometimes with a vague, slightly darker brown band just below the periphery. Surface dull or slightly silky above the periphery, somewhat shiny below. Spire slightly to moderately raised; apex rounded. Whorls: Top whorls slightly convex, outer whorls moderately convex above the periphery, convex below, periphery slightly and obtusely angular (more distinctly so in juveniles). Suture impressed. Sculpture. Protoconch with minute, dense radial wrinkles (just visible at 40x magnification), also with a few more distinct folds proximally and towards the transition to the teleoconch. Teleoconch. Radial sculpture: Growth lines, at uneven intervals raised or developing into slight, inconspicuous, low riblets. Spiral sculpture: Above the periphery widely and unevenly spaced, wavy, and locally braided shallow grooves, with the distance from the suture increasingly oblique down to well below the periphery, basal side of the sell with similar, truly spiral sculpture again. Aperture broadly and obliquely crescent-shaped, inside white or with a slight purplish hue. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open but very narrow, party covered by the peristome. Dimensions. Height up to 20.5 mm; width up to 40 mm; ratio height/width 0.62–0.63; diameter of the first two whorls 3.0–3.5 mm, 7.8–8.5 mm; number of whorls up to 4; height aperture up to 20.5 mm; width aperture up to 22.5 mm.

Animal leaving the shell fully exposed when creeping; mantle hardly projecting beyond the shell outline. Body mottled grey on the sides, dark grey-brown on the back, with two dull pink lines extending backwards from the upper tentacles, and one similar line on the tail.

Distribution in Sabah. Common in W. Elevation range: 300–2700 m. In (disturbed) primary forest on limestone and sandstone/shale bedrock. Endemic to Sabah.

Note. Shell morphology and the whorl count resemble the shell of various semi-slugs, but *Kalamantania* is a snail according to the definition of this category in the key to the families: The mantle does not at all cover the shell in creeping animals.

Genus Rhinocochlis Thiele, 1931

Diagnosis for the Sabah species. Shell sinistral, translucent. Periphery acutely keeled. Radial sculpture: Virtually absent, some growth lines only. Peristome slightly spreading or not on the palatal and basal side, angular or



Fig. 143, a. *Everettia corrugata corrugata* Laidlaw, 1937; b. *Everettia interior* Liew, Schilthuizen & Vermeulen, 2009; c. *Everettia jucunda* (L Pfeiffer, 1864); d. *Everettia jucundior* Liew, Schilthuizen & Vermeulen, 2009; e. *Everettia monticola* Liew, Schilthuizen & Vermeulen, 2009; f. *Everettia planispira* Liew, Schilthuizen & Vermeulen, 2009; g. *Everettia layanglayang* Liew, Schilthuizen & Vermeulen, 2009; h. *Everettia subconsul* (E A Smith, 1887).

with a drawn-out beak on the palatal side. Shell up to 34.5 mm wide.

Rhinocochlis chlorosoma (Vermeulen, Liew & Schilthuizen, 2015) (fig. 145a, 146a–c, map 30f)

Dyakia chlorosoma Vermeulen et al. 2015: 37. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., Ulu Kimanis, along Keningau-Kimanis road.

Rhinocochlis moluensis auct. Schilthuizen 2004: 95; Liew et al. 2010: Online Supporting Information, Appendix S1.

[Not Dyakia moluensis Godwin-Austen].

Description. Shell sinistral, large, very thin, translucent, pale yellowish green. Surface glossy. Spire conical with slightly concave (juveniles) to slightly convex (adults) sides; apex not protruding, narrowly rounded. Whorls: Top whorls moderately convex, outer whorls flat above the periphery, last whorl convex below, periphery pinched and acutely keeled. Sculpture. Protoconch with a few flat radial folds, no other sculpture. Teleoconch. Radial sculpture: First whorls slightly crenellated immediately below the suture, all whorls with approx. evenly spaced, slightly raised, weak growth lines, shell surface, particularly on the last whorl, distinctly undulated following the growth lines. Spiral sculpture absent, some shells with an inconspicuous spiral undulation on the last whorl. Aperture the shape of a circular sector, angular on the palatal side. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus closed. Dimensions. Height up to 14 mm; width up to 32 mm; ratio height/width 0.55–0.57; diameter of the first three whorls 1.9–2.1 mm, 3.5–4 mm, 8.0–8.3 mm respectively; number of whorls up to c. 4; height aperture up to 10.5 mm; width aperture up to 14.0 mm.

Animal (pale) green, shining through the shell a bright green. Tentacles green, whitish, yellowish or brownish distally.

Distribution in Sabah. Highlands, rather common: Mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 1200–2200 m. In primary forest on sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Dyakia moluensis Godwin-Austen, 1891 (Sarawak), has a thicker shell with spiral color bands, and a fine, somewhat spaced spiral striation on the upper and lower surface.

Note. Apart from the absence of a beaked peristome, the species generally resembles *Rhinocochlis nasuta*. The anatomy, too, more resembles *R. nasuta* than *Dyakia* (T–S Liew).

Rhinocochlis nasuta (Metcalfe, 1852)

(fig. 145b, 146d–f, map 30f)

Thiele 1931: 633; Saul 1967: 110; Vermeulen 1996b: 286; Panha & Ung 2001: 95; Marzuki et al. 2021: 90. – Helix nasuta Metcalfe 1852 (1851): 70; Pfeiffer 1853: 203; Reeve 1853 (1851–1854): Pl. 157, fig. 1031. – Helix (Corasia) nasuta (Metcalfe) Pfeiffer 1855b: 144. – Helicostyla (Corasia) nasuta (Metcalfe) H & A Adams 1858: 193. – Ryssota nasuta (Metcalfe) Wallace 1865: 407. – Nanina (Dyakia) nasuta (Metcalfe) Von Martens 1867: 224; Tenison Woods 1888: 1025; Von Martens 1908: 285. – Nanina nasuta (Metcalfe) Issel 1874: 393. – Nanina (Ariophanta) nasuta (Metcalfe) Pfeiffer & Clessin 1881: 56. – Dyakia nasuta (Metcalfe) Godwin-Austen 1891: 32; Schepman 1896: 153; Kobelt 1897: 53; Von Martens 1908: 261. – Amphidromus (Pseudopartula) nasuta (Metcalfe) Pilsbry 1901 (1901–1902): 12; 1904: 47. – Pseudopartula nasuta (Metcalfe) Von Martens 1908: 262. – Type from 'Borneo'.

Cross diagnosis. Among Borneo snails, adult shells are uniquely identified by the sharp peripheral keel combined with the drawn-out beak on the lateral side of the peristome. Juveniles without the beak resemble *Rhinocochlis chlorosoma* but can be distinguished by the presence of a fine and dense spiral striation.

Description. Shell sinistral, large, very thin, translucent, pale yellowish green to white. Surface with a silky luster above, shiny below. Spire rather low-conical with approx. straight to slightly convex sides; apex narrowly rounded. Whorls: Top whorls moderately convex, other whorls slightly convex on both sides of the periphery, and slightly depressed just above the periphery (periphery pinched); periphery distinctly and acutely keeled. Suture not impressed. Sculpture. Protoconch smooth, slightly crenellated just below the suture, with a few weak spiral grooves towards the teleoconch. Teleoconch. Radial sculpture: Weak growth lines, locally slightly raised. Spiral sculpture: Fine, densely placed, shallow but continuous grooves above the periphery, similar but somewhat coarser and more widely spaced grooves below the periphery. A very fine (just visible at 40x magnification) granular sculpture is also present above the periphery, on the outer whorls. Aperture the shape of a circular sector, with a drawn-out, distally slightly recurved beak where the peripheral keel meets the peristome. Peristome a thin, dull glazing on the parietal side, elsewhere not thickened, slightly spreading. Umbilicus open, but very narrow. Dimensions. Height 9.0–12.5 mm; width 22.5–34.5 mm (width without spur on palatal peristome 21.2–33.0 mm); ratio height/width 0.35–0.46; diameter of the first three whorls 1.7–2.0 mm, 3.0–4.2 mm, 6.5–9.2 mm respectively; number of whorls



Fig. 144, a. *Everettia dominiki* Liew, Schilthuizen & Vermeulen, 2009; b. *Kalamantania whiteheadi* (Godwin-Austen, 1891); c–e. *Kalamantania whiteheadi* (Godwin-Austen, 1891), c. Frontal view, shell 22 mm high, d. Umbilical view, e. Apical view.



Fig. 145, a. Rhinocochlis chlorosoma (Vermeulen, Liew & Schilthuizen, 2015); b. Rhinocochlis nasuta (Metcalfe, 1852).

4 5/8–5 1/4; umbilicus c. 0.5 mm diam.; height aperture 7.0–8.5 mm; width aperture 13.0–20.0 mm. Animal green, shining through the shell a bright green. Tentacles somewhat yellowish to orange-red. *Distribution in Sabah*. Scattered localities in W, mainly highlands: Mount Tambuyukon, mount Kinabalu, Crocker range; elsewhere in Maliau basin. Elevation range: 600–2300 m. In primary forest, on sandstone/shale bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Family ENDODONTIDAE Pilsbry, 1895

Diagnosis for the Sabah species. Snails. Shell with up to 3 1/2–6 1/2 slowly expanding whorls. Shell dextral, minute or very small, approx. as wide as high or wider than high (but higher than wide in *Sitalinopsis conulus*); spire (depressed) conical to (depressed) ovoid; last whorl rounded to angular or keeled at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth lines, in many species (locally) raised to fine riblets with or without a periostracal crest, spiral sculpture present, inconspicuous to distinct, in many species including distinct spiral threads. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed, or open, narrow to wide. Dimensions: Adults up to 1.4–3.2 mm high, 1.7–3.5 mm wide.

Genus Philalanka Godwin-Austen, 1898

Diagnosis for the Sabah species. Shell conical to conical-ovoid, whorls somewhat depressed or not. Teleoconch: Radial sculpture prosocline, indistinct to coarse growth lines only, or with fine growth lines grading into rather densely placed, rather distinct riblets. Last whorl without spiral threads, or with 1–6 distinct spiral threads (next to much finer spiral threads), the lowermost around the periphery, the others above the periphery and often interrupted. Umbilicus open, narrow, or closed.

Notes. 1. Species with a single, conspicuous spiral thread and species without a spiral thread resemble *Kaliella* (Chronidae) but have a wider umbilicus. *Philalanka anomphala* is the exception, with a closed umbilicus, but this has rather coarse, unevenly spaced growth lines, unlike any Borneo *Kaliella*.

- 2. The species in Group 2, *Philalanka thienemanni* excepted, resemble *Microcystina* (Ariophantidae), but generally have coarser and more uneven radial sculpture. *Microcystina consobrina* resembles *Philalanka malimgunung*; it differs by the densely and evenly placed radial riblets on the upper side of the last whorl which do not continue beyond the periphery on to the lower side.
- 3. Type of the genus is *Philalanka secessa* Godwin-Austen, 1898, from Sri Lanka, a species somewhat resembling *P. thienemanni*, with a single peripheral thread on the last whorl. Species with more than one spiral thread

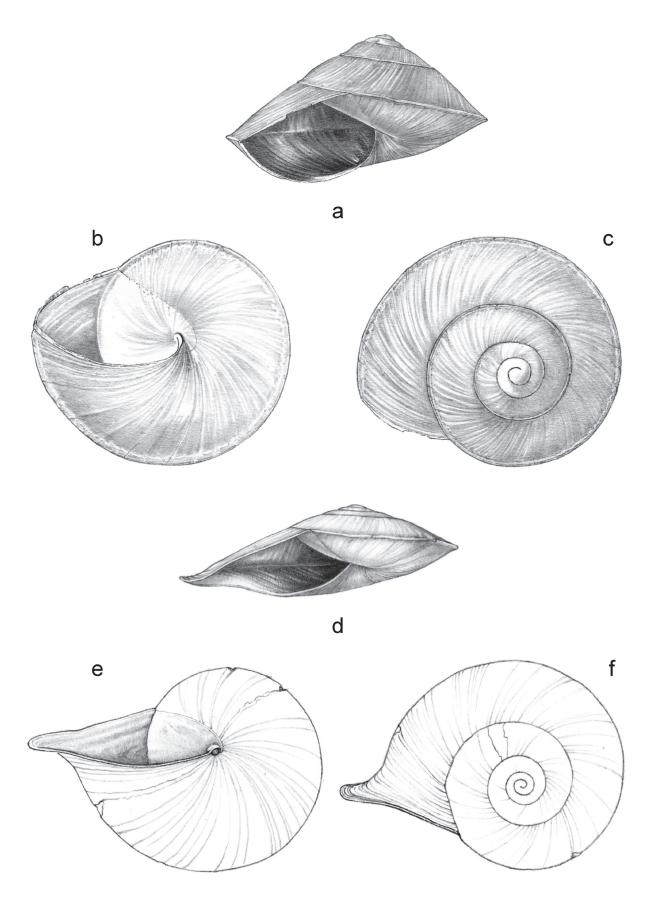


Fig. 146, a–c. *Rhinocochlis chlorosoma* (Vermeulen, Liew & Schilthuizen, 2015), a. Frontal view, shell 14 mm high, b. Umbilical view, c. Apical view; d–f. *Rhinocochlis nasuta* (Metcalfe, 1852), d. Frontal view, shell 10.5 mm high, e. Umbilical view, f. Apical view.

(comparable to *P. kusana*) are included by Gude (1914), next to species without any spiral sculpture (comparable to *P. malimgunung*).

- 4. We follow Godwin-Austen (1897–1914: 188), by placing *Philalanka* in Endodontidae. MolluscaBase (accessed 1/2021) places it in Charopidae.
 - 5. We divide the genus into two informal groups.

KEY TO THE GROUPS

1 – Last whorl with 2 or more distinct spiral threads

Group 1

1 – Last whorl with 1 spiral thread, or without a spiral thread

Group 2

Group 1

Philalanka kusana (Aldrich, 1889)

(fig. 147a-c, 148a, map 31a)

Vermeulen & Whitten 1998: 92, 148; Maassen 2001: 95; Schilthuizen & Rutjes 2001: 420; Schilthuizen et al. 2002: 256, 257, 258; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Tan et al. 2012: 102; Schilthuizen et al. 2013: Online supplementary data; Vermeulen et al. 2015: 64; Marzuki et al. 2021: 78. – *Trochomorpha kusana* Aldrich 1889: 24. – *Sitala kusana* (Aldrich) Godwin-Austen 1891: 40. – Type from Indonesia, SE Kalimantan.

Sitala quadricarinata Gude 1917: 315. – Type from Borneo.

Philalanka carinigera auct. Saul 1967: 110.

[Not Philalanka kusana auct. Vermeulen & Whitten 1998: 92, 148; = Sitala tjibodasensis Leschke].

[Not Sitala carinigera Tapparone-Canefri].

Description. Shell very small, thin, translucent to opaque, light brown to pale yellow-corneous to white. Surface shiny. Spire conical with slightly convex sides, sometimes conical-ovoid; apex rounded. Whorls convex, rounded or slightly angular because of the presence of strong spiral threads, somewhat flattened below the low-ermost spiral thread, sometimes somewhat flattened above the upper spiral thread. Sculpture. Protoconch without radial sculpture or with some subordinate wrinkles; with (1–)4–6(–9) inconspicuous to distinct, thin spiral threads. Teleoconch. Radial sculpture: Fine growth lines, locally grading into somewhat spaced riblets, most distinct below the suture. Spiral sculpture: Last whorl with (2–)3(–4) distinct, narrow threads (when 2: 1 above and 1 below the periphery; when 3–4: 1 at the periphery, 1 well below, and 1–2 above), the lowermost coinciding with the suture of the penultimate whorl; between the threads often (traces of) a fine, rather dense to moderately spaced striation; below the lowermost spiral thread a similar moderately to widely spaced spiral striation which gradually disappears towards the umbilicus. Aperture broadly crescent-shaped to obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 3.2 mm; width up to 3.5 mm; diameters of the first four whorls 0.6–0.8 mm, 1.0–1.3 mm, 1.6–2.0 mm, 2.1–2.7 mm respectively; number of whorls up to 5 1/2; height aperture up to 1.1 mm; width aperture up to 1.6 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1200 m. In primary and secondary forest, shrubby regrowth, rock outcrops, on sandstone/shale and limestone bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Malaysia (Peninsula), Singapore, Indonesia (Sumatra; E-wards to West Papua).

Variability. Most individuals of *Philalanka kusana* have 3 spiral threads, but large samples usually include a few specimens with only 2 spiral threads. In a few samples from the Crocker range, Kappes (unpublished report, Leiden University) finds two separate species within our concept of *P. kusana*, based on molecular data and supported by slight differences in protoconch sculpture. We find a wide variability in protoconch sculpture and cannot accordingly divide all material available. Aldrich (1889) describes the shell color as light brown. All specimens seen by us range from pale yellow-corneous to white.

Similar species elsewhere. Philalanka tjibodasensis (Leschke, 1914) (Indonesia, Java) has a comparable size and mode of coiling (diameter of the first four whorls c. 0.6 mm, 1.1 mm, 1.6 mm, 2.4 mm respectively). It differs by having flattened protoconch whorls without spiral sculpture. Philalanka carinifera (Stoliczka, 1873), from Peninsular Malaysia, is of similar shape, but smaller (height up to 2 mm, and width up to 2.1 mm, at 5 3/8 whorls). It is also more densely coiled (diameter of the first four whorls 0.4–0.5 mm, 0.70–0.85 mm, 1.05–1.20 mm, 1.4–1.6 mm respectively).

Philalanka moluensis (E A Smith, 1893)

(fig. 147d–e, map 31b)

Schilthuizen et al. 2002: 256, 257; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 67;

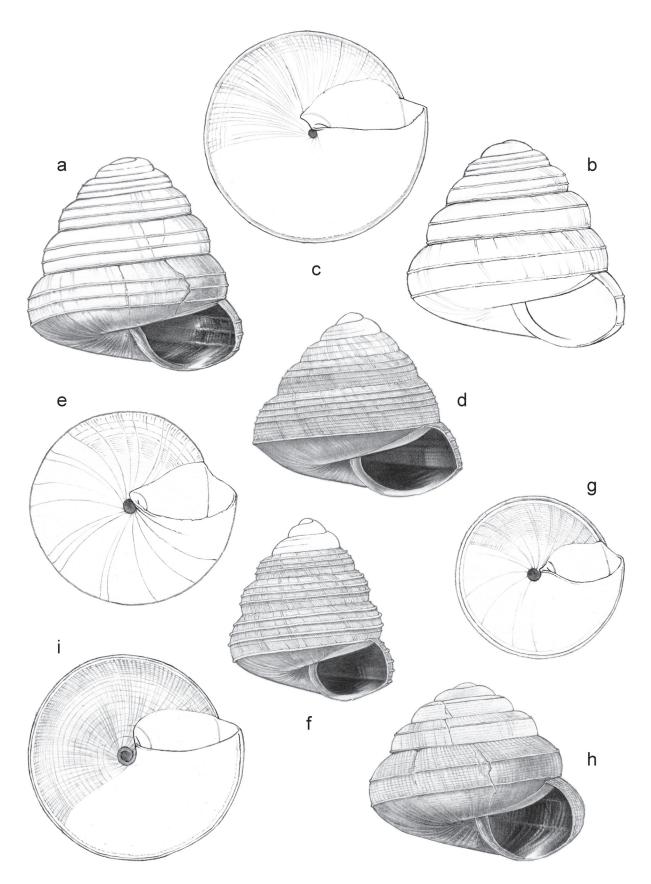


Fig. 147, a–c. *Philalanka kusana* (Aldrich, 1889), frontal views, a. Shell 3.4 mm high, b. Shell 3.4 mm high, c. Umbilical view; d–e. *Philalanka moluensis* (E A Smith, 1893), d. Frontal view, shell 2.3 mm high, e. Umbilical view; f–g. *Philalanka obscura* Vermeulen, Liew & Schilthuizen, 2015, f. Frontal view, shell 2.1 mm high, g. Umbilical view; h–i. *Philalanka tambunanensis* Vermeulen, Liew & Schilthuizen, 2015, h. Frontal view, shell 1.9 mm high, i. Umbilical view.

Marzuki et al. 2021: 79. – *Sitala moluensis* Smith 1893b: 343; Von Martens 1908: 261. – *Liardetia moluensis* (E A Smith) Saul 1967: 110. – Type from Malaysia, Sarawak, Mulu area. *Sitala inaequisculpta* Smith 1895: 112. – Type from Malaysia, Sarawak, 'mount Rabong'.

Cross diagnosis. Differs from *Philalanka kusan*a and *P. tambunanensis* by the shell color. Resembles *Kaliella microconus*, differs by its much coarser and less evenly spaced spiral threads, and more convex whorls.

Description. Shell very small, rather thin, approx. opaque, brown, very rarely yellowish. Surface about dull or with a silky luster above the periphery, glossy below. Spire conical with approx. straight or slightly convex sides; apex rounded. Whorls convex, approx. rounded. Sculpture. Protoconch without radial sculpture or with some subordinate wrinkles; with 9–12 inconspicuous to distinct, very fine, thin spiral threads. Teleoconch. Radial sculpture: Densely placed, very fine (just visible at 40x magnification), narrow riblets that may be inconspicuous locally. Spiral sculpture: Last whorl with a distinct thread coinciding with the suture of the penultimate whorl, above this 2–4 slightly less distinct threads with a very fine (just visible at 40x magnification) striation in between, particularly towards the periphery; below the periphery up to 4 fine threads close to it, with very fine striation in between. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.9 mm; width up to 2.8 mm; diameters of the first four whorls 0.55–0.65 mm, 0.9–1.1 mm, 1.35–1.55 mm, 1.9–2.1 mm respectively; number of whorls up to 5 7/8; height aperture up to 1.2 mm; width aperture up to 1.6 mm.

Distribution in Sabah. Widespread, rather common; not in N. Elevation range: 0–1100 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Also in Sarawak. Endemic to Borneo.

Philalanka obscura Vermeulen, Liew & Schilthuizen, 2015

(fig. 147f–g, map 31c)

Vermeulen et al. 2015: 69. – Type from Indonesia, Kalimantan Timur, Sangkulirang Peninsula, Meweding Cave near village Tabalar Ulu.

Philalanka obscura, unavailable name, Clements et al. 2008: 2762.

Cross diagnosis. Shares the shell color with *Philalanka moluensis*, differs by the absence of a fine spiral striation in between the spiral threads above the periphery, except for a few subordinate threads. Next to this, the shells are usually more elongated conical, and the spiral threads are thicker.

Description. Shell very small, rather thin, approx. opaque, (dark) brown, sometimes yellowish. Surface approx. dull or with a silky luster above the periphery, glossy below. Spire conical with approx. straight or slightly convex sides; apex rounded. Whorls convex, approx. rounded. Sculpture. Protoconch without radial sculpture or with some subordinate wrinkles; with 9–12 inconspicuous to distinct, very fine, thin spiral threads. Teleoconch. Radial sculpture: Densely placed, very fine (just visible at 40x magnification), narrow riblets which may be inconspicuous locally. Spiral sculpture: Last whorl with a distinct thread coinciding with the suture of the penultimate whorl, above this 3–4 about equally distinct threads, and in between up to 2 less distinct ones; below the lowermost thread a very fine striation close to it, sometimes with up to 4 slightly coarser threads interspersed. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.7 mm; width up to 2.4 mm; diameters of the first four whorls 0.5–0.65 mm, 0.85–1.00 mm, 1.15–1.35 mm, 1.5–1.8 mm respectively; number of whorls up to 5 3/4; height aperture up to 0.9 mm; width aperture up to 1.3 mm.

Distribution in Sabah. Widespread, scattered localities; not in N. Elevation range: 0–600 m. In primary and secondary forest on limestone and sandstone/shale bedrock. Also in Kalimantan. Endemic to Borneo.

Philalanka tambunanensis Vermeulen, Liew & Schilthuizen, 2015

(fig. 147h–i, map 31d)

Vermeulen et al. 2015: 63. - Type from Malaysia, Sabah, Interior Prov., mount Trus Madi slopes, Gua Loloposon.

Cross diagnosis. Differs from *Philalanka kusana* by the more distinct spiral striation next to the two spiral threads, as well as a more distinct radial sculpture. As a result, the shell is not shiny, but has a silky luster. *Philalanka tambunanensis* usually has two spiral threads; *P. kusana* usually has three, sometimes two.

Description. Shell very small, thin, translucent to opaque, pale brown- or yellow-corneous to white. Surface with a silky luster. Spire conical with straight or slightly convex sides; apex widely rounded. Whorls convex, rounded. Sculpture. Protoconch without radial sculpture or with some very fine, subordinate wrinkles; with 10–15 rather distinct, thin spiral threads. Teleoconch. Radial sculpture: Fine growth lines grading into rather densely placed, rather distinct riblets, most distinct below the suture; the interstices between these riblets cut into the crests of the spiral striation. Spiral sculpture: Last whorl with (1–)2 inconspicuous to distinct, narrow threads (1 above the periphery, sometimes absent; 1 below the periphery, coinciding with the suture of the penultimate whorl); next

to these a distinct, fine, rather dense striation present, sometimes less conspicuous just below the suture; below the lowermost thread the striation is (somewhat) more widely spaced and gradually disappears towards the umbilicus. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus open, rather narrow. Dimensions. Height up to 2.3 mm; width up to 2.5 mm; diameters of the first four whorls 0.55–0.80 mm, 0.95–1.20 mm, 1.45–1.80 mm, 2.0–2.3 mm respectively; number of whorls up to 5; height aperture up to 1.0 mm; width aperture up to 1.3 mm.

Distribution in Sabah. Rare in W: Mount Kinabalu, mount Tambuyukon, upper Padas. Elevation range: 500–1200 m. In damp primary forest around streams, on limestone and sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. Philalanka carinifera (Stoliczka, 1873) (Peninsular Malaysia), is more densely coiled (diameters of the first four whorls 0.4–0.5 mm, 0.70–0.85 mm, 1.05–1.20 mm, 1.4–1.6 mm respectively), and has a shiny surface with inconspicuous sculpture only, apart from the spiral threads.

Group 2

Check also:

Philalanka tambunanensis and *P. kusana* (Group 1). Rare specimens of these species have 1 spiral thread; these differ from *P. anomphala* by the open umbilicus, from *P. rugulosa* by the more densely coiled spire (diameter of third whorl 1.45–2.0 mm, versus 2.25–2.60 mm), and from *P. thienemanni* by the more distinctly convex whorls.

Philalanka anomphala Vermeulen, Liew & Schilthuizen, 2015

(fig. 149a-b, map 31d)

Vermeulen et al. 2015: 71. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., Mesilau trail. *Philalanka* sp. 1 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. The closed umbilicus distinguishes the species within Group 2.

Description. Shell very small, thin, hardly translucent, yellow-corneous. Surface glossy. Spire depressed-conical with slightly convex sides, apex somewhat flattened. Whorls convex, rounded. Sculpture. Protoconch surface almost smooth, virtually without radial sculpture, and very fine (just visible at 40x magnification), dense spiral striation towards the periphery. Teleoconch. Radial sculpture: Predominant, rather coarse, moderately spaced but unevenly placed, usually somewhat sunk growth lines above the periphery, which are less conspicuous below the periphery. Spiral sculpture: last whorl with a thin, inconspicuous (conspicuous in juveniles) thread following the periphery and coinciding with the suture of the penultimate whorl; above this, traces of very fine (just visible at 40x magnification), rather dense striation, below the periphery with a similar, but widely spaced, striation. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus closed, rimate in juveniles. Dimensions. Height up to c. 1.75 mm; width up to c. 2.3 mm; diameters of the first three whorls c. 0.75 mm, c. 1.25 mm, c. 1.9 mm respectively; number of whorls up to c. 3 5/8; height aperture up to 1.0 mm; width aperture up to 1.2 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2000–2400 m. In montane forest on sandstone/shale bedrock. Endemic to Sabah.

Similar species elsewhere. The closed umbilicus also distinguishes *Philalanka anomphala* from *P. lieftincki* Van Benthem Jutting, 1953 (Indonesia, Ambon), and *P. micromphala* Van Benthem Jutting, 1952 (Indonesia, Java).

Philalanka malimgunung Vermeulen, Liew & Schilthuizen, 2015

(fig. 149c–d, map 31e)

Vermeulen et al. 2015: 73. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., summit trail. *Philalanka* sp. 2 Liew et al. 2010: Online Supporting Information, Appendix S1.

Description. Shell minute, very thin, hardly translucent, pale yellow-brown, yellow-corneous below. Surface with a silky luster. Spire (low-)conical with approx. straight sides; apex rounded. Whorls: Protoconch whorls moderately convex, teleoconch whorls convex, rounded (angular in juveniles), suture somewhat impressed. Sculpture. Protoconch without radial sculpture; with inconspicuous, very fine (just visible at 40x magnification) and dense spiral striation towards the periphery. Teleoconch. Radial sculpture: Somewhat predominant, rather distinct, unevenly spaced, slightly raised growth lines, which are less conspicuous towards the umbilicus. Spiral sculpture: very fine (just visible at 40x magnification), dense striation above the periphery, which is continuous on the top whorls but more patchy on the last whorl; with a similar but somewhat more widely spaced striation below the periphery. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus open, rather narrow. Dimensions. Height up to 1.4 mm; width up to 1.9 mm; diameters of the first three whorls 0.45–0.50 mm,





Fig. 148, a. Philalanka kusana (Aldrich, 1889); b. Philalanka rugulosa Vermeulen, Liew & Schilthuizen, 2015.

0.85-1.00 mm, 1.40-1.55 mm respectively; number of whorls up to c. 3 1/2; height aperture up to 0.8 mm; width aperture up to 0.9 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3100–4100 m. In subalpine vegetation on granodiorite bedrock. Endemic to Sabah.

Similar species elsewhere. Differs from the extralimital species listed under *Philalanka rugulosa* by the lack of a peripheral thread.

Philalanka rugulosa Vermeulen, Liew & Schilthuizen, 2015

(fig. 148b, 149e–f, map 31f)

Vermeulen et al. 2015: 73. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., summit trail. *Philalanka* sp. 3 Liew et al. 2010: Online Supporting Information, Appendix S1.

Cross diagnosis. Distinctly larger than *Philalanka malimgunung*, best expressed in the diameter of the third whorl (2.25–2.60 mm, versus 1.40–1.55 mm). *Kaliella scandens* and *K. doliolum* are similar in shape but have more evenly spaced radial ribs.

Description. Shell very small, very thin, hardly translucent, yellowish brown. Surface with a silky luster. Spire (low) conical with slightly convex sides; apex rounded. Whorls: Protoconch whorls moderately convex; teleoconch whorls convex above and below the periphery, periphery rounded to slightly angular (in adults; more distinctly angular in juveniles, suture somewhat impressed. Sculpture. Protoconch almost smooth, with the slightest traces of a radial sculpture, and of a very fine, dense spiral striation. Teleoconch. Radial sculpture: Rather distinct, unevenly spaced, somewhat raised growth lines, grading into more evenly and rather densely placed, low riblets; towards the umbilicus the growth lines tend to become less conspicuous. Spiral sculpture: Last whorl sometimes with a thin, inconspicuous peripheral thread coinciding with the suture of the penultimate whorl; some traces of a fine, dense striation below this thread. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.7 mm; width up to 3.4 mm; diameters of the first three whorls 0.65–0.75 mm, 1.2–1.4 mm, 2.25–2.60 mm respectively; number of whorls up to c. 4 1/4; height aperture up to 1.5 mm; width aperture up to 1.75 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 2900–4100 m. In subalpine vegetation on granodiorite bedrock. Endemic to Sabah.

Similar species elsewhere. Philalanka lieftincki Van Benthem Jutting, 1953 (Indonesia, Ambon) looks similar but is smaller (shell 1.5–1.9 mm high, at 4–4 1/2 whorls, versus shell up to 2.7 mm high at 4 1/4 whorls). Philalanka micromphala Van Benthem Jutting, 1952 (Indonesia, Java) is of similar shape and size, but has a more angular last whorl with a distinct peripheral thread, a finer radial sculpture and a more depressed aperture (aperture 1.1–1.2 mm high at a shell height of 2.1–2.7 mm, versus aperture c. 1.5 mm high at a shell height of c. 2.7 mm).

Philalanka thienemanni B Rensch, 1932

(fig. 149g-h, map 32a)

Rensch 1932: 105; Van Benthem Jutting 1952: 404; 1959: 137; Vermeulen & Whitten 1998: 94, 149; Schilthuizen 2004: 95; Vermeulen et al. 2015: 70. – Type from Indonesia, Java.

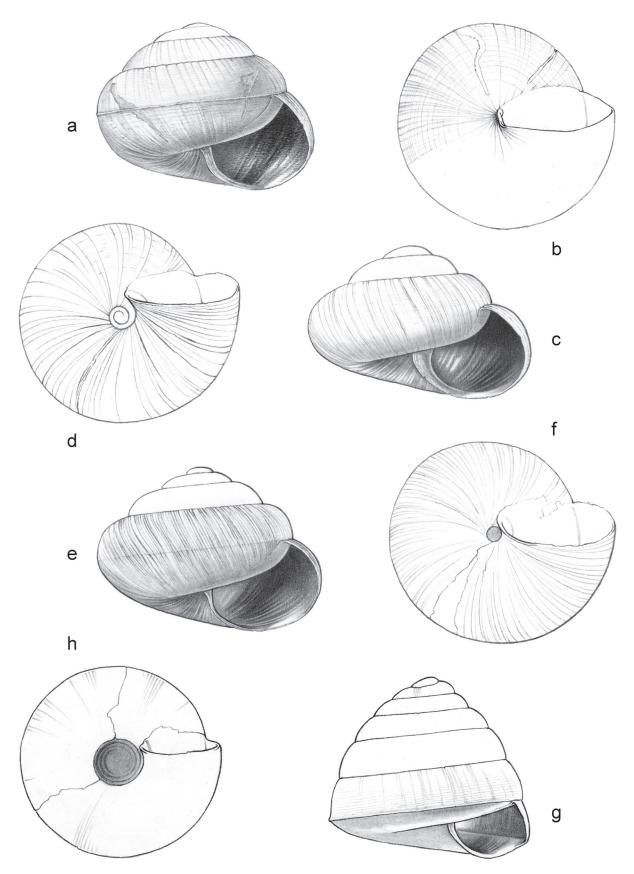


Fig. 149, a–b. *Philalanka anomphala* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 1.9 mm high, b. Umbilical view; c–d. *Philalanka malimgunung* Vermeulen, Liew & Schilthuizen, 2015, c. Frontal view, shell 1.4 mm high, d. Umbilical view; e–f. *Philalanka rugulosa* Vermeulen, Liew & Schilthuizen, 2015, e. Frontal view, shell 2.7 mm high, f. Umbilical view; g–h. *Philalanka thienemanni* B Rensch, 1932, g. Frontal view, shell 2.3 mm high, h. Umbilical view.

Cross diagnosis. The approx. conical spire distinguishes the species within Group 2.

Description. Shell very small, very thin, translucent, pale yellow-corneous to white. Surface glossy. Spire conical with convex sides to almost conical-ovoid; apex rounded. Whorls: Protoconch whorls convex, teleoconch whorls moderately convex, last whorl rounded or slightly angular because of the presence of a strong spiral thread. Sculpture. Protoconch smooth or with 1–6 very inconspicuous, thin spiral threads. Teleoconch. Radial sculpture: Locally with a few inconspicuous, well-spaced growth lines, locally also with very fine (barely visible at 40x magnification), densely placed riblets. Spiral sculpture: Last whorl with a distinct, thick peripheral thread coinciding with the suture of the penultimate whorl; next to this thread (traces of) very fine, inconspicuous, well-spaced, very thin threads except in the umbilical region; with or without (traces of) an even finer (just visible at 40x magnification), dense striation in between these threads, especially above the peripheral thread. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, wide. Dimensions. Height up to 2.35 mm; width up to 2.6 mm; diameters of the first four whorls 0.5–0.6 mm, 0.90–1.05 mm, 1.3–1.6 mm, 1.80–2.15 mm respectively; number of whorls 6; height aperture up to 0.8 mm; width aperture up to 1 mm.

Distribution in Sabah. Widespread but rare: Crocker range, Segaliud Lokan. Elevation range: 500–1700 m. Found in damp (disturbed) primary forest on sandstone/shale bedrock. Distribution elsewhere: Thailand, Indonesia (Java, Bali, Flores).

Variability. Shells from Thailand have a slightly more distinct spiral sculpture, particularly on the lower surface, than shells from Java. The Borneo shells are intermediate in this respect.

Genus *Sitalinopsis* Thiele, 1930 (= *Queridomus* Iredale, 1937) (= *Thysanota* auct. Vermeulen et al., 2015)

Diagnosis for the Sabah species. Shell conical, with almost straight sides, with depressed whorls. Teleoconch: Radial sculpture prosocline, consisting of densely placed to moderately spaced, fine riblets, the most prominent with a narrow, interrupted periostracal crest. Last whorl with 2–3 distinct spiral threads (next to several much finer spiral threads), the lowermost around the periphery, the others above the periphery and often interrupted. Umbilicus open, narrow, or closed.

- *Notes.* 1. Differs from *Philalanka* by the presence of a narrow periostracal crest on the most prominent radial riblets. The crest easily wears off; *Sitalinopsis* particularly resembles *Philalanka kusana* and *P. tambunanensis* in the placement of the most prominent spiral threads on the last whorl but differs by the more prominent additional sculpture. *Sitalinopsis* also differs from *Kaliella* (Chronidae) by the generally more prominent sculpture.
- 2. Vermeulen et al. (2015: 74) place the two species below in *Thysanota* Albers, 1860, based on shell resemblance. Gittenberger et al. (2019: 24) find that a Maldives species which strongly resembles the Sabah ones has a radula different from that of an Indian species generally included in *Thysanota*. They place the three in *Sitalinopsis* Thiele, 1931 (type species *S. conulus*).
- 3. MolluscaBase (accessed 1/2021) places *Sitalinopsis* in Ariophantidae, and *Thysanota*, including *conula* and *grenvillei*, in Charopidae. Our placement in Endodontidae is a convenience, based on the shell shape resembling *Philalanka*.

Sitalinopsis conulus (W T Blanford, 1865)

(fig. 150a, map 32b)

Thiele 1931: 612; Gittenberger et al. 2019: 24. – *Nanina conula* Blanford 1865: 73. – *Helix conulus* (W T Blanford) Pfeiffer 1868: 89. – *Trochomorpha (Kaliella) conula* (W T Blanford) Pfeiffer & Clessin 1881: 83. – *Kaliella conulus* (W T Blanford) Godwin-Austen 1883 (1882–1888): 71; Blanford & Godwin-Austen 1908: 272. – *Queridomus conulus* (W T Blanford) Clements et al. 2008: 2762. – *Thysanota conula* (W T Blanford) Vermeulen et al. 2015: 75. – Type from India, Arakan.

Sitala fimbriosa Quadras & Von Möllendorff 1894a: 89. – Kaliella fimbriosa (Quadras & Von Möllendorff) Rensch
1932: 67. – Sitalinopsis fimbriosa (Quadras & Von Möllendorff) Rensch 1935: 332. – Liardetia fimbriosa
(Quadras & Von Möllendorff) Van Benthem Jutting 1950: 410; Maassen 1997: 61. – Queridomus fimbriosus
(Quadras & Von Möllendorff) Vermeulen & Whitten 1998: 104, 152; Maassen 2001: 95. – Type from Philippines, Negros.

Sitala elatior Bavay & Dautzenberg 1908: 232. – Type from Vietnam, Phu-Quoc-Oai.

Thysanota elegans Preston 1909: 135; Gude 1914: 13; Naggs & Raheem 2000: iii, 23. – Type from Sri Lanka.

Description. Shell very small, rather thin, somewhat translucent or opaque, pale brown to white. Surface about dull or with a silky luster above the periphery, shiny below. Spire conical with approx. straight sides; apex rounded. Whorls: Protoconch whorls convex, teleoconch whorls moderately convex, (moderately) angular at the periphery,

above the periphery slightly rounded or almost flat, below the periphery with a second, moderate edge at a distance from the periphery, below this almost flat. Sculpture. Protoconch: Radial sculpture absent or subordinate; with 10–15 distinct, fine, rather densely placed, thin spiral threads. Teleoconch. Radial sculpture: Growth lines above the periphery and particularly below the suture, grading into rather densely placed to moderately spaced, fine, narrow riblets at approx. even distances. Spiral sculpture: Last whorl with a distinct peripheral thread, below the periphery with a second, equally distinct thread at a distance from the periphery, and coinciding with the suture of the penultimate whorl; next to these two with numerous much finer, well-spaced threads, which become finer and more widely spaced towards the suture and towards the umbilicus, and which may form slight nodes where they cross the radial sculpture. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus closed, or open, narrow. Dimensions. Height up to 2.3 mm; width up to 1.6 mm; diameters of the first four whorls 0.40–0.45 mm, 0.60–0.65 mm, 0.80–0.95 mm, 1.05–1.30 mm respectively; number of whorls up to 6 1/2; height aperture up to 0.5 mm; width aperture up to 0.9 mm.

Distribution in Sabah. Sapulut only. Elevation range: 400–500 m. In logged forest on limestone bedrock, elsewhere in a range of disturbed environments; drought tolerant. Distribution elsewhere: India, Vietnam, Malaysia (Peninsula), Indonesia (S-wards to Java, E-wards to Halmahera).

Variability. The relative width of the shell shows some variability: Some shells are slightly higher than wide; others are distinctly higher than wide.

Sitalinopsis grenvillei (Brazier, 1876)

(fig. 150b, map 32b)

Gittenberger et al. 2019: 24. – *Helix grenvillei* Brazier 1876: 104. – *Queridomus grenvillei* (Brazier) Iredale 1937: 322; Solem 1988: 552. – *Thysanota grenvillei* (Brazier 1876) Vermeulen et al. 2015: 76. – Type from Australia, Queensland, Cape York Peninsula.

Sitala homfrayi Godwin-Austen 1895: 448. – Philalanka homfrayi Gude 1914: 16. – Type from India, Andaman Islands.

Cross diagnosis. More depressed conical than *Sitalinopsis conulus*, with more rapidly expanding whorls (diameter of the fourth whorl 1.85–2.40 mm, versus 1.05–1.30 mm).

Description. Shell very small, rather thin, somewhat translucent or opaque, (pale) brown. Surface about dull or with a silky luster above the periphery, shiny below. Spire somewhat depressed conical with approx. straight sides; apex rounded. Whorls: Protoconch convex, teleoconch moderately convex, (moderately) angular at the periphery, above the periphery rounded or with a second, slight angle at a distance from the periphery, below the periphery rounded. Sculpture. Protoconch: Radial sculpture absent; whorls with 7–10 rather distinct, very fine, well-spaced, thin spiral threads. Teleoconch. Radial sculpture: Growth lines, above the periphery grading into densely placed, rather evenly spaced, fine, narrow riblets. Spiral sculpture: Last whorl with a distinct peripheral spiral thread coinciding with the suture of the penultimate whorl, above this, 1(–2) less distinct threads as well as numerous very fine spiral threads, which form minute nodes where they cross the radial sculpture, the threads more widely spaced towards the upper suture; below the peripheral thread with finer threads close to it, as well as a fine, continuous, moderately spaced striation over most of the lower surface. Aperture obtusely quadrangular, peristome not widened, not thickened. Umbilicus open, narrow. Dimensions. Height up to 2.0 mm; width up to 2.5 mm; diameters of the first four whorls 0.4–0.5 mm, 0.70–0.95 mm, 1.15–1.50 mm, 1.85–2.40 mm respectively; number of whorls up to 4 5/8; height aperture up to 0.85 mm; width aperture up to 1.25 mm.

Distribution in Sabah. Rare in E: Baturong-Madai, Segarong hills. Elevation range: 0–200 m. In disturbed primary forest, and in shrubby coastal vegetation, on limestone bedrock. Distribution elsewhere: Vietnam, Australia.

Notes. 1. The Borneo material is virtually identical with the Australian shell shown in Solem (1988: 552), and with material collected by the first author in Ha Long Bay, northern Vietnam. Australian shells have periostracal hairs where the more distinct spiral threads cross the radial ribs. In some Vietnamese shells these hairs are fused to low, erose periostracal crests on the spiral threads. In the Bornean shells, all periostracum has worn off.

2. The species is now known from widely distant localities from Vietnam to Australia. It is probably a wide-spread element of the coastal fauna but appears rare.

Family **FERUSSACIIDAE** Bourguignat, 1883

Diagnosis for the Sabah species. Snails. Shell with up to 4 1/8–4 1/2 slowly expanding whorls. Shell dextral, minute to very small, distinctly higher than wide; spire elongated ovoid-cylindrical to cylindrical; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines; spiral sculpture very fine. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus closed.

Dimensions: Adults 1.5–4.2 mm high, 0.4–1.3 mm wide.

Note. Superficially resembling Sabah Achatinidae, particularly the genera with small shells; the differences are given under the genera below.

Genus *Cecilioides* Férussac, 1814

Diagnosis for the Sabah species. Spire ovoid-cylindrical. Shell up to 4.2 mm high.

Note. Differs from Sabah Achatinidae, particularly the genera with small shells, by the presence of fine spiral sculpture. Also, the shell is more narrowly coiled, and the basal corner of the aperture is broadly rounded, not obtusely angular as in Achatinidae.

Cecilioides caledonica (Crosse, 1867)

(fig. 150c, map 32c)

Franc 1956: 109; Vermeulen & Whitten 1998: 86, 147; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data. – *Geostilbia caledonica* Crosse 1867: 186; Maassen 2001: 83. – *Cionella (Cecilioides) caledonica* (Crosse) Pfeiffer & Clessin 1881: 333. – *Cecilioides (Geostilbia) caledonica* (Crosse) Van Benthem Jutting 1964: 60. – Type from New Caledonia.

Description. Shell very small, thin, translucent, pale corneous. Surface shiny. Spire elongated ovoid-cylindrical with approx. straight sides; apex not drawn-out, broadly rounded. Whorls moderately convex, suture somewhat impressed. Sculpture. Protoconch approx. smooth. Teleoconch. Radial sculpture inconspicuous, a few weak growth lines. Spiral sculpture: A very fine striation, locally present. Aperture obliquely drop-shaped, broadly rounded at the base, peristome not thickened nor spreading, columellar side straight. Umbilicus closed. Dimensions. Height up to 4.2 mm; width up to 1.3 mm; number of whorls up to 4 1/4, height aperture up to 1.6 mm; width aperture up to 0.8 mm.

Distribution in Sabah. Scattered localities in E. Elevation range 0–200 m. Disturbed environments, from forest to denuded land, on limestone bedrock. Distribution elsewhere: Widespread in SE Asia.

Genus *Coilostele* Benson, 1864

Diagnosis for the Sabah species. Spire cylindrical. Shell 1.5–1.6 mm high.

Note. Differs from Sabah Achatinidae, in particular the genera with small shells, by its much smaller size (Height 1.5–1.6 mm, width c. 0.4–0.5 mm at c. 4 whorls, versus the smallest Sabah achatinid, *Opeas hannense*, height 2.0–2.5 mm, width 1.2–1.5 mm at c. 4 whorls), and by its cylindrical spire.

Coilostele inquirenda B Rensch, 1935

(fig. 150d, map 32d)

Rensch 1935: 321; Schilthuizen et al. 2011: 5. – Type from Indonesia, Timor.

Description. Shell minute, thin, translucent, white. Surface glossy. Spire cylindrical, apex rounded. Whorls slightly convex, suture somewhat impressed. Sculpture. Protoconch approx. smooth. Teleoconch. Radial sculpture: Raised growth lines, locally developing into low, rather densely placed, rounded riblets. Spiral sculpture: Locally traces of a subordinate, very fine striation. Aperture somewhat obliquely ovate, broadly rounded at the base. Peristome not thickened, not spreading, forming a thin glazing on the parietal side. Umbilicus closed. Dimensions. Height 1.5–1.6 mm; width 0.4–0.5 mm; ratio height/width 3.7–3.8; number of whorls c. 4 1/8; height aperture 0.5–0.6 mm; width aperture 0.3–0.4 mm.

Distribution in Sabah. Banggi island only. Elevation: 0 m. Only found in beach drift material. Distribution elsewhere: Indonesia (Timor).

Note. Status unclear. Like *Rhytida* (*Macrocycloides*) *densesculpta* (see Excluded Species), originally described from beach drift material, and never found in situ. We cannot match it with a marine species; therefore, we include it as a terrestrial.

Family GASTRODONTIDAE Tryon, 1866

Diagnosis for the Sabah species. Snails. Shell with up to 3 7/8–4 5/8 slowly expanding whorls. Shell dextral, (very) small, distinctly wider than high; spire depressed-conical; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth lines, locally raised to low riblets; spiral sculpture absent or in-

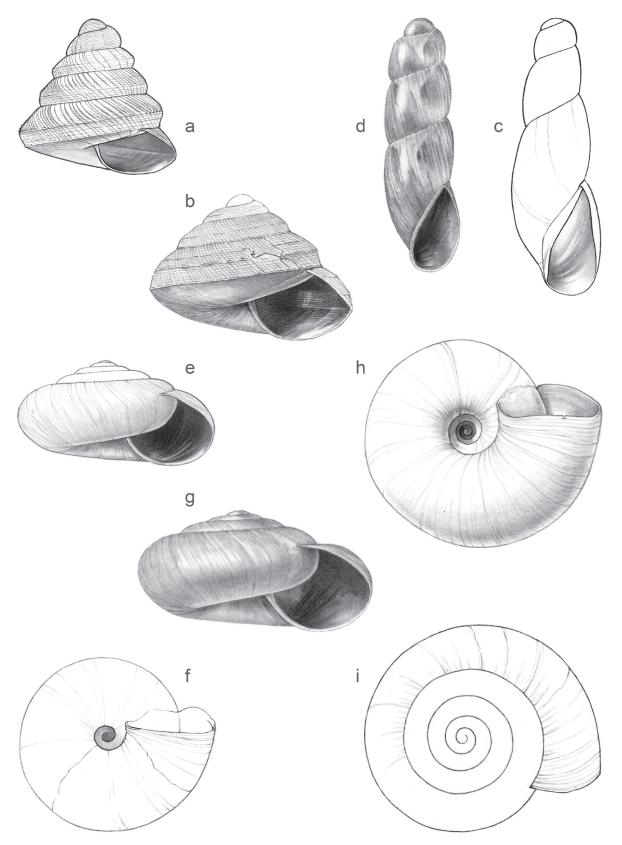


Fig. 150, a. *Sitalinopsis conulus* (W T Blanford, 1865), frontal view, shell 1.5 mm high; b. *Sitalinopsis grenvillei* (Brazier, 1876), frontal view, shell 1.9 mm high; c. *Cecilioides caledonica* (Crosse, 1867), frontal view, shell 3.5 mm high; d. *Coilostele inquirenda* B Rensch, 1935, frontal view, shell 1.55 mm high; e–f. *Zonitoides arboreus* (Say, 1817), e. Frontal view, shell 2.5 mm high, f. Umbilical view; g–i. *Zonitoides nitidus* (O F Müller, 1774), g. Frontal view, shell 3.5 mm high, h. Umbilical view, i. Apical view.



Fig. 151. Zonitoides nitidus (O F Müller, 1774).

conspicuous. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus open, (rather) wide. Dimensions: Adults 2.2–4.7 mm high, 4.2–6.8 mm wide.

Genus *Zonitoides* Lehmann, 1862

Notes. 1. General shape like *Microcystina* or *Macrochlamys* (Ariophantidae); differs by the umbilicate shell. Some lenticular Charopidae also have an umbilicate shell but are smaller and have a more distinct sculpture; *Leucocharopion* has a smaller, white shell.

2. Capinha et al. (2014) describe the potential of Zonitoides as invasive species in tropical montane forest.

Zonitoides arboreus (Say, 1817)

(fig. 150e–f, map 32e)

Cowie 1997: 41; Capinha et al. 2014: 605. – *Helix arboreus* Say 1817: Helix sp. 2, 7th page, pl. 4, fig. 4. – Type from USA.

Description. Shell dextral, very small, transparent, pale yellow-corneous. Surface glossy. Spire depressed-conical with approx. straight sides, apex narrowly rounded. Whorls convex above and below the periphery, periphery evenly rounded. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Rather densely placed, unevenly spaced, slightly raised, wide and rounded riblets above the periphery, which are less distinct below the periphery. Spiral sculpture. Traces of a very fine spiral striation locally present in some shells, just visible at 40x magnification. Aperture broadly crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, rather wide. Dimensions. Height 2.2–2.7 mm; width 4.2–5.0 mm; ratio height/width 0.49–0.58; diameter of the first four whorls 0.8–1.0 mm, 1.5–1.8 mm, 2.7–3.0 mm, 4.3–4.9 mm respectively; number of whorls 3 7/8–4 3/8; umbilicus 0.6–1.0 mm diam., or 13–20 % of the shell width; height aperture 1.4–1.7 mm; width aperture 1.9–2.2 mm.

Animal grey, without a spot of different color in the mantle.

Distribution in Sabah. Highlands, rare: Mount Tambuyukon, mount Kinabalu. Elevation range: 1300–2200 m. Disturbed primary forest near habitation, damp roadside with high grass and shrubs, on sandstone/shale bedrock. Introduced. Distribution elsewhere: Cosmopolitan. Natural range: N and central America, Caribbean.

Zonitoides nitidus (O F Müller, 1774)

(fig. 150g-i, 151, map 32f)

Lehmann 1862: 111; Capinha et al. 2014: 605. - Helix nitida Müller 1774: 32. - Type from Germany.

Cross diagnosis. Larger than Zonitoides arboreus (Shell width 5.9–6.8 mm, versus 4.2–5.0 mm), with the outer whorls wider (diameter 4th whorl 4.9–5.9 mm, versus 4.3–4.9 mm) and a wider umbilicus (22–26 % of the shell width, versus 13–20 %). Living animals differ from Z. arboreus by the presence of a yellow or orange spot in the mantle, which is visible through the transparent shell, close to the peristome and between the periphery and the suture (see fig. 151).

Description. Shell dextral, small, transparent, yellow-corneous to brown-corneous, often slightly paler on the basal side. Surface glossy. Spire depressed-conical with approx. straight sides, apex narrowly rounded. Whorls convex above and below the periphery, periphery evenly rounded. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Rather densely placed, approx. evenly or unevenly spaced, slightly raised, wide and rounded riblets above the periphery, which are less distinct below the periphery. Spiral sculpture absent. Aperture broadly crescent-shaped. Peristome a thin glazing on the parietal side, elsewhere not thickened, not spreading. Umbilicus open, wide. Dimensions. Height 3.5–4.7 mm; width 5.9–6.8 mm; ratio height/width 0.56–0.59; diameter of the first four whorls 0.9–1.0 mm, 1.7–2.0 mm, 3.1–3.6 mm, 4.9–5.9 mm respectively; number of whorls 4 1/4–4 5/8; umbilicus 1.3–1.7 mm diam., or 22–26 % of the shell width; height aperture 2.1–2.7 mm; width aperture 2.8–3.1 mm.

Animal very dark or black. A yellow or orange spot in the mantle is visible through the translucent shell, close to the peristome and between the periphery and the suture.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 1600–2000 m. Damp cultivated area cleared in primary forest, on sandstone/shale bedrock. Introduced. Distribution elsewhere: Cosmopolitan. Natural range: Holarctic.

Family **HELICARIONIDAE** Bourguignat, 1877

Diagnosis for the Sabah species. Snails or semi-slugs with the shell partly covered by the mantle. Shell dextral, small, wider than high, inflated lenticular with a very large aperture; last whorl rounded at the periphery. Aperture without teeth. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines; spiral sculpture inconspicuous. Peristome on the palatal side not thickened, not spreading. Umbilicus closed or rimate. Dimensions: Adults up to 7.9–9.0 mm high, 10.0–12.3 mm wide, and with up to 2 1/2–4 1/8 (rather) rapidly expanding whorls.

Notes. 1. We include four species with shells of generally 'helicarionid' appearance (small, glassy, generally smooth and with few rapidly expanding whorls) but which are otherwise incompletely known: We have not dissected living specimens of the two *Helicarion* sp., and we have little information on the shells of the two *Sabalimax* sp. Further investigation is needed.

- 2. Tillier & Bouchet (1989) place Sabalimax in Trochomorphidae.
- 3. MolluscaBase (accessed 1/2021) places Helicarion in Helicarionidae, Sabalimax in Euconulidae.

Genus Helicarion Férussac, 1821

Diagnosis for the Sabah species. Shell with up to 3 5/8-4 1/8 whorls.

Note. Helicarion borneense has a rather small shell, compared to the size of the animal, see fig. 154a. The mantle edge has no lobes covering the shell. *Helicarion albellus* (Von Martens, 1867), a Java species with a very similar shell, has 5 mantle lobes largely covering the shell in creeping animals; see Van Benthem Jutting (1948: 416). Despite convergence of shell morphology the two species may be of different affinity.

Helicarion borneense (Pfeiffer, 1857)

(fig. 152a-c, 154c, map 33a)

Von Martens 1867: 186; Issel 1874: 391; Pfeiffer & Clessin 1881: 31; Tenison Woods 1888: 1010; Godwin-Austen 1891: 24; Von Martens 1908: 259. – *Vitrina borneensis* Pfeiffer 1857 (1856a): 324; 1858 (1854–1860): 100; 1859: 793; Reeve 1862b: Pl. 6, fig. 41. – Type from 'Borneo'.

Cross diagnosis. Resembles *Helicarion dyakanum*, differs by the glossy shell surface, with an only slightly elevated spire.

Description. Shell small, very thin, transparent, pale green. Surface glossy. Outline inflated lenticular, spire slightly elevated. Whorls moderately convex. Sculpture. Protoconch without radial riblets; with traces of very fine densely placed spiral grooves (just visible at 40x magnification). Teleoconch with few scattered, inconspicuous growth lines. Spiral sculpture: Just below the suture a few very fine, widely spaced spiral grooves which fade

out further away from the suture, surface otherwise without spiral sculpture. Aperture broadly crescent-shaped, peristome not widened, not thickened. Umbilicus closed, columellar side of the peristome only slightly thickened and widened. Dimensions. Height up to 9.0 mm; width up to 12.3 mm; ratio height/width 0.73–0.81; diameters of the first three whorls 1.1–1.4 mm, 2.5–3.3 mm, 6.2–8.5 mm respectively; number of whorls up to 3 5/8; height aperture up to 7.0 mm; width aperture up to 7.5 mm.

Distribution in Sabah. Highlands: Crocker range, Trus Madi range, Upper Padas. Elevation range: 900–1200 m. In damp primary forest near stream, on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo.

Helicarion dyakanum (Godwin-Austen, 1891)

(fig. 152d–f, map 33b)

Microcystis dyakana Godwin-Austen 1891: 37; Smith 1898a: 28; Marzuki et al. 2021: 94. – *Microcystina dyakana* (Godwin-Austen) Von Martens 1908: 260. – Type from Malaysia, Sarawak, 'Busan Hills'.

Cross diagnosis. Vitrinula padasensis has a larger 1st whorl, while the next whorls expand more slowly (diameter of the 1st and the 4th whorls: 2.1–2.2 mm and 12.8–14.0 mm, versus 1.0–1.4 mm and 9.5–9.8 respectively).

Description. Shell small, very thin, translucent, very pale brown to yellow-green, or white. Surface slightly silky. Outline inflated lenticular, spire moderately elevated. Whorls moderately convex. Sculpture. Protoconch without radial riblets; with or without traces of very fine, densely placed spiral grooves (just visible at 40x magnification). Teleoconch with few scattered, inconspicuous growth lines. Spiral sculpture: Just below the suture very fine, moderately spaced spiral grooves which often disappear towards the last whorl, and which, further away from the suture, become finer and are placed more closely together, lower down on the whorls small, local patches of even finer spiral striation (just visible at 40x magnification); umbilical area with or without patches with a few slightly coarser striae. Aperture broadly crescent-shaped with the basal peristome distinctly curved towards the columellar corner; peristome not widened, not thickened. Umbilicus rimate because largely covered by the gradually widened columellar side of the peristome. Dimensions. Height up to 7.9 mm; width up to 10.0 mm; ratio height/width (0.68–)0.70–0.82; diameters of the first four whorls 1.0–1.4 mm, 2.4–3.0 mm, 5.5–6.8 mm, 9.5–9.8 mm respectively; number of whorls up to 4 1/8; height aperture up to 5.0 mm; width aperture up to 5.8 mm.

Distribution in Sabah. Highlands: Mount Trus Madi only. Elevation range: 1000–1100 m. In damp primary forest near stream, on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Variability. In Sabah known from one sample with subadult shells. The description includes Sarawak material. The type has a slightly less elevated shell than usual, see ratio height/width between brackets.

Genus Sabalimax Tillier & Bouchet, 1989

Diagnosis for the Sabah species. Shell with up to c. 2 1/2 whorls.

Animal. Tail concave along the median line, sides with a conspicuous 'fishbone' pattern: flattened ridges which start on the edge of the median furrow and run obliquely backwards to the foot edge. Shell visible through a lumen in the mantle; mantle-edge with 4 lobes: 2 anterior and 2 posterior.

Anatomy. Penis with 1–2 long lateral appendices which are all (partially) included in a muscular sheath which is open at the apex. Vas deferens inserted at the apex of the epiphallus.

Sabalimax cyanantyx Tillier & Bouchet, 1989

(fig. 153a-b, 154d, map 33b)

Tillier & Bouchet 1989 (1988): 285; Vermeulen 1996b: 288. - Type from Malaysia, Sabah, mount Kinabalu.

Description. Shell small, very thin, transparent, corneous. Surface glossy. Outline inflated lenticular; spire slightly elevated. Whorls convex. Sculpture. Protoconch smooth. Teleoconch with few scattered, inconspicuous growth lines. Spiral sculpture absent. Aperture: peristome not widened, not thickened. Umbilicus closed. Dimensions. Number of whorls approx. 2 3/8.

Animal rather slender; tail rather long. Mantle approx. smooth; part surrounding the shell with 4 lobes, the 2 anterior approx. circular, rather small, the right not covering the shell apex when extended. Color pink to pale yellow with extensive dark, blue-grey to blackish, markings: Tentacles dark, anterior part of body unevenly shaped dark blotches, posterior part without markings along the median line, with wide, sharply outlined, densely placed oblique lines along the sides, down to the foot margin; foot and foot margin dark, visceral mass shining through the shell dark brown with yellow specks; mantle with distinct dark blotches.

Anatomy. Gametolytic sac distinctly longer than the gametolytic duct. Penis with one lateral appendix which is entirely included in the penis sheath.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3200–3300 m. In primary woodland on granodiorite bedrock. Endemic to Sabah.

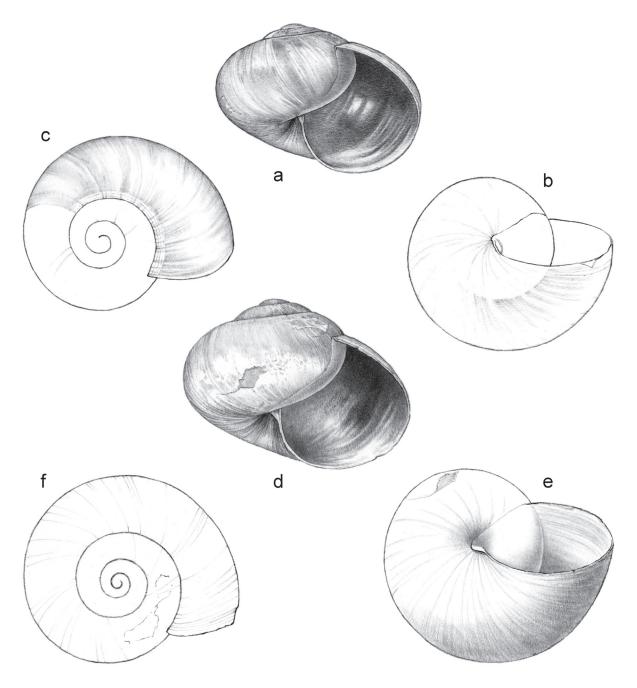


Fig. 152, a–c. *Helicarion borneense* (L Pfeiffer, 1857), a. Frontal view, shell 4.5 mm high, b. Umbilical view, c. Apical view; d–f. *Helicarion dyakanum* (Godwin-Austen, 1891), d. Frontal view, shell 5.2 mm high, e. Umbilical view, f. Apical view.

Note. We have insufficient information on the external appearance of the shell to provide a full description.

Sabalimax pantherina Tillier & Bouchet, 1989

(fig. 154c–d, map 33c)

Tillier & Bouchet 1989 (1988): 281; Vermeulen 1996b: 288; Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, mount Kinabalu.

Cross diagnosis. Differs from *Sabalimax cyanantyx* by the anterior mantle lobes, which are crescent-shaped and obtuse (versus circular) and cover the shell apex when extended. Anatomically, it is characterized by the upper penis appendage which widely protrudes from the penis sheath (included in *S. cyanantyx*).

Description. Shell small, very thin, transparent, corneous. Surface glossy. Outline inflated lenticular, spire slightly elevated. Whorls convex. Sculpture. Protoconch with very fine, inconspicuous spiral striation. Teleoconch

with few scattered, inconspicuous growth lines. Spiral sculpture very fine, inconspicuous, on top whorls only. Aperture: peristome not widened, not thickened. Umbilicus closed. Dimensions. Width up to 6.5 mm; number of whorls up to 2 1/2.

Animal rather slender; tail long. Mantle approx. smooth; part surrounding the shell with 4 lobes, the 2 anterior approx. crescent-shaped, obtuse, large, the right covering the shell apex when extended. Color pale yellow with extensive dark markings.

Anatomy. Gametolytic sac approx. as long as the gametolytic duct, or slightly longer. Penis with two lateral appendices, the upper widely protruding from the penis sheath.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3000–3400 m. In primary woodland on granodiorite bedrock. Endemic to Sabah.

Note. We have insufficient information on the external appearance of the shell to provide a full description.

Family **HELICODISCIDAE** Pilsbry, 1927

Diagnosis for the Sabah species. Snails. Shell with 3 3/8–6 1/2 slowly expanding whorls. Shell dextral, minute, wider than high, discoid with a slightly raised spire; last whorl narrowly rounded above the periphery. Teleoconch sculpture: Radial sculpture consisting mainly of growth lines; spiral sculpture fine but distinct. Aperture with teeth. Peristome on the palatal side thickened, spreading. Umbilicus open, wide. Dimensions: Height 0.7–0.8 mm; width 1.6–1.7 mm.

Genus Stenopylis Fulton, 1914

Stenopylis coarctata (Von Möllendorff, 1894)

(fig. 154a-b, map 33d)

Fulton 1914: 164; Van Benthem Jutting 1952: 405; Solem 1988: 535; Maassen 1997: 56; Vermeulen & Whitten 1998: 94, 149; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data. – *Plectopylis coarctata* Von Möllendorff in Quadras & Von Möllendorff 1894b: 113. – Type from Philippines, Bohol, Panglao.

Description. Shell minute, rather thin, translucent, white. Surface shiny. Outline discoid with a slightly raised spire. Protoconch somewhat inflated, its whorls wider than the first teleoconch whorls. Whorls broadly rounded but narrowly rounded and widest well above the periphery. Suture impressed. Sculpture. Protoconch about smooth or with an inconspicuous sculpture resembling that of the teleoconch. Teleoconch. Radial sculpture: Unevenly spaced, subordinate growth lines. Spiral sculpture: Fine but rather distinct, rather well spaced spiral threads. Aperture reniform. Peristome distinctly thickened and spreading all around, developed into a thick, upright lip on the parietal side. Aperture inside with 2 parietales. Umbilicus open, wide. Dimensions. Height 0.7–0.8 mm; width 1.6–1.7 mm; number of whorls 3 1/4–3 1/2, height and width aperture c. 0.6 mm.

Distribution in Sabah. Rare on the islands, though locally in large numbers: Banggi island, Tun Sakaran Marine Park. Elevation range: 0–100 m. In coastal woodland, also in degraded coastal vegetation. Distribution elsewhere: Vietnam (N part), Indonesia (Sumatra, Java), E-wards to Australia, Solomon Islands.

Family **PHILOMYCIDAE** Gray, 1847

Diagnosis for the Sabah species. Slugs without shells.

Animal semi-circular in section, not much flattened, not dorsally keeled. No caudal horn. Mantle covering the entire dorsal side of the animal when creeping except for part of the head with the tentacles, the lower sides and the tail apex, mantle fused to the body (the edges cannot be lifted), laterally rounded; surface smooth. Ventral side undivided. Tentacles 4; upper pair with eyes; lower pair without lobes. Anus and respiratory pore on the right side, at some distance distal to the head, in a deep sinus in the notum (notum: See fig. 170a).

Note. Revision adapted from Schilthuizen et al. (2008).

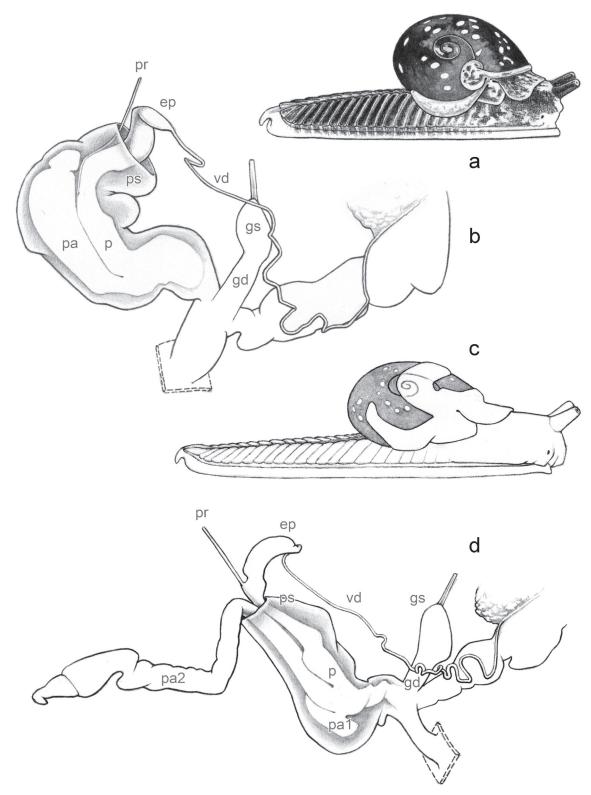


Fig. 153, a–b. *Sabalimax cyanantyx* Tillier & Bouchet, 1989, a. Animal, reconstructed from specimen preserved in alcohol and with colour pattern added from photograph, right lateral view, animal 17.5 mm long, b. Distal part of genitals; c–d. *Sabalimax pantherina* Tillier & Bouchet, 1989, c. Animal, reconstructed from specimen preserved in alcohol, right lateral view, animal 20.5 mm long, d. Distal part of genitals. Abbreviations; ep = epiphallus; gs = gametolytic sac; gd = gametolytic duct; p = penis; pa = penis appendix; pr = penis retractor muscle; ps = penis sheath; vd = vas deferens.

Genus Meghimatium Van Hasselt, 1823

Meghimatium pictum (Stoliczka, 1872)

(fig. 154e, map 33e)

Wiktor et al. 2000: 12; Schilthuizen & Liew 2008: 304. – *Philomycus pictus* Stoliczka 1873: 30; Maassen 2001: 123 (*'Philomucus'*). – Type from Malaysia, Penang island.

Description. Animal slender when creeping, with a distinctly tapering tail. Anus and respiratory pore at 10–20 % of the body length, measured from the head. Body, including upper tentacles, white to grey to pale brown to orange, with 3 vague to sharply outlined, usually very uneven and often interrupted, grey, brown or black longitudinal stripes, with spots in between or interconnected by unevenly distributed transverse markings; these patterns in some specimens so dense that the entire surface is marbled or mottled. Dimensions. Creeping animals up to 45 mm long, up to 7 mm wide.

Distribution in Sabah. Rare in W: Mount Kinabalu, Crocker range, Trus Madi range; in E Tawau hills only. Elevation range: 400–1700 m. Primary forest on sandstone/shale and volcanic bedrock. Distribution elsewhere: Nepal, China, Laos, Malaysia (Peninsula).

Note. Because of molecular and anatomical data, Schilthuizen & Liew (2008) suspect that *Meghimatium pictum* is a compound entity in the present delimitation.

Meghimatium striatum Van Hasselt, 1823

(fig. 154f, map 33f)

Van Hasselt 1823: 232; Laidlaw 1937: 179; Van Benthem Jutting 1952: 425; 1959: 137; Vermeulen 1996b: 289; Cowie 1997: 26; Schilthuizen & Liew 2008: 303; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Philomycus striatus* (Van Hasselt) Von Martens 1867: 178. – Type from Indonesia, Java.

Cross diagnosis. Differs from *Meghimatium pictum* by 3–5 longitudinal black stripes, with the median 3 are wide, rather even and uninterrupted, and sharply outlined.

Description. Animal slender when creeping, with a distinctly tapering tail. Anus and respiratory pore at 10–15 % of the body length, measured from the head. Body, including upper tentacles, orange-yellow to brown to pink, with 3–5 wide, rather even, sharply outlined, black longitudinal stripes, if 5 stripes the outer, close to the mantle edge, narrow and/or interrupted; sometimes also with fine, uneven transverse markings between the stripes. Dimensions. Creeping animals up to 45 mm long, up to 7 mm wide.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 1500–2600 m. Primary forest on sandstone/shale bedrock. Distribution elsewhere: Japan to Indonesia (Java, Sulawesi).

Meghimatium uniforme Laidlaw, 1937

(fig. 154g–h, map 34a)

Laidlaw 1937: 177; Vermeulen 1996b: 289; Schilthuizen & Liew 2008: 303; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Philomycus uniformis* (Laidlaw) Maassen 2001: 124 ('*Philomucus*'). – Type from Malaysia, Sabah, mount Kinabalu, Pakka.

Cross diagnosis. Differs from other Sabah *Meghimatium* by the position of the anal and respiratory pore, at c. 33 % of the body length, measured from the head (versus 10–20 %), and by the dark upper tentacles. Also, the body is uniformly colored, usually without dark markings.

Description. Animal rather slender when creeping, slightly to moderately tapering towards the tail. Anus and respiratory pore at c. 33 % of the body length, measured from the head. Body white, blue-grey, pale brown or orange-yellow, usually without dark spots, sometimes with some tiny black specks approx. arranged along 3 longitudinal lines. Upper tentacles dark-colored. Dimensions. Creeping animals up to 30 mm long, up to 8 mm wide.

Anatomy. Penis and vas deferens distinctly shorter than in other Sabah Meghimatium.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 3100–3600 m. Primary forest on granodiorite bedrock. Endemic to Sabah (see note).

Note. We assume that the record from Peninsular Malaysia in Maassen (2001) is erroneous.

Family **PUNCTIDAE** Morse, 1864

Diagnosis for the Sabah species. Snails. Shell with up to 3 1/2–3 3/4 slowly expanding whorls. Shell dextral, minute, wider than high, spire depressed conical to lenticular; last whorl rounded at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth lines, locally raised to fine riblets the coarsest of which have a

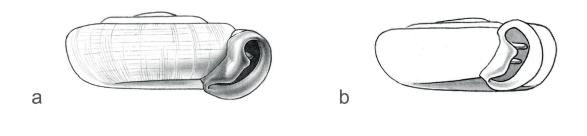




Fig. 154, a–b. *Stenopylis coarctata* (Von Möllendorff, 1894), a. Frontal view, shell 0.8 mm high, b. Oblique right lateral view; c. *Helicarion borneense* (L Pfeiffer, 1857), juvenile; d. *Sabalimax cyanantyx* Tillier & Bouchet, 1989; e. *Meghimatium pictum* (Stoliczka, 1872); f. *Meghimatium striatum* Van Hasselt, 1823; g–h. *Meghimatium uniforme* Laidlaw, 1937.

periostracal crest, spiral sculpture present, fine. Aperture without teeth. Peristome on the palatal side not thickened, not spreading. Umbilicus open, narrow to wide. Dimensions: Adults up to 0.8–1.25 mm high, 1.2–2.3 mm wide.

Genus *Paralaoma* Iredale, 1913

Notes. 1. Resembles *Sundacharopa* (Charopidae) and *Microcystina* (Ariophantidae), differs by the radial ribs, the most prominent of which have a narrow periostracal crest. This easily wears off in empty shells. Such shells can generally be recognized by the more uneven radial sculpture, with the most prominent ribs well-spaced, with less conspicuous riblets in between.

2. The protoconch sculpture easily wears off, leaving a slightly rough surface without features.

Paralaoma albella Vermeulen & Liew, new species

(fig. 155a–b, map 34b)

Type from Indonesia, Sumatra, N part, Gua Liangdehar, near Kota Buluh, 40 km NW of Brastagi (holotype BOR/MOL 14842; paratypes JV 5021/6 shells).

Paralaoma caputspinulae auct. Vermeulen & Whitten 1998: 94, 149 (partly, excluding fig.); Schilthuizen 2004: 95 (partly).

Paralaoma sp. Liew et al. 2010: Online Supporting Information, Appendix S1.

[Not Paralaoma caputspinulae (Reeve)].

Cross diagnosis. Characterized within Sabah *Paralaoma* by its protoconch without spiral sculpture. Also, it differs from the about equally large *P. gracilitesta* by the shouldered whorls, which are well-rounded at the periphery, the wider umbilicus (27–30 % of the shell width, versus 10–20 %), and the much finer, sometimes almost absent teleoconch sculpture. Shares the umbilical width with *P. servilis*, differs by the less rapidly expanding whorls (diameter of the first three whorls 0.30–0.35 mm, 0.65–0.70 mm, 0.95–1.05 mm respectively, versus 0.40–0.50 mm, 0.90–0.95 mm, 1.45–1.70 mm).

Description. Shell minute, thin, slightly translucent, white or pale yellowish. Surface slightly shiny. Spire low-conical. Whorls shouldered just below the suture, otherwise well-rounded. Sculpture. Protoconch finely punctate; no other sculpture visible at 40x magnification. Teleoconch. Radial sculpture very inconspicuous to locally distinct, unevenly spaced radial ribs some of which, at wide intervals, have a narrow periostracal crest; radial ribs are equally distinct above and below the periphery; locally in between these very fine, densely placed, low secondary riblets above the periphery. Spiral sculpture a very fine (just visible at 40x magnification) and dense spiral striation, slightly more prominent but equally dense below the periphery. Aperture broadly crescent-shaped, peristome not thickened, not spreading. Umbilicus wide. Dimensions. Height up to 0.8 mm; width up to 1.2 mm; diameter of the first three whorls 0.30–0.35 mm, 0.65–0.70 mm, 0.95–1.05 mm respectively; umbilicus 27–30 % of the shell width; number of whorls up to 3 1/2; height aperture up to 0.45 mm; width aperture up to 0.5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 900–2200 m. In (disturbed) primary forest on limestone and sandstone/shale bedrock. Distribution elsewhere: Thailand, Indonesia (Sumatra, Bali).

Name derivation. From the diminutive of albus (Latin) = white.

Paralaoma angusta Vermeulen, Liew & Schilthuizen, 2015

(fig. 155c–d, map 34b)

Vermeulen et al. 2015: 109; Marzuki et al. 2021: 79. – Type from Malaysia, Sabah, Kiansom Falls near Kota Kinabalu.

Cross diagnosis. Characterized among Sabah *Paralaoma* by the narrow umbilicus (5–6 % of the shell width, versus 10–30 %), the presence of radial riblets on the protoconch, and the coarse and widely spaced spiral sculpture on the lower surface.

Description. Shell minute, thin, slightly translucent, yellowish brown. Surface shiny. Spire low-conical to lenticular. Whorls well-rounded. Sculpture. Protoconch with densely placed radial riblets which are particularly distinct towards the periphery, with fine, rather densely placed spiral grooves cutting into the crests of the radial riblets. Teleoconch. Radial sculpture locally distinct, widely spaced radial ribs with a periostracal crest, which gradually disappear towards the umbilicus; in between these very fine, densely placed, low secondary riblets above the periphery. Spiral sculpture: Spiral threads, as fine and as densely placed as the secondary radial riblets, above the periphery, grading into widely spaced, rather distinct grooves towards the umbilicus. Aperture crescent-shaped, peristome not thickened, not spreading. Umbilicus narrow. Dimensions. Height up to 1.1 mm; width up to 1.6 mm; diameter of the first three whorls 0.4–0.45 mm, 0.75–0.8 mm, 1.25–1.3 mm respectively; umbilicus 5–6 % of the

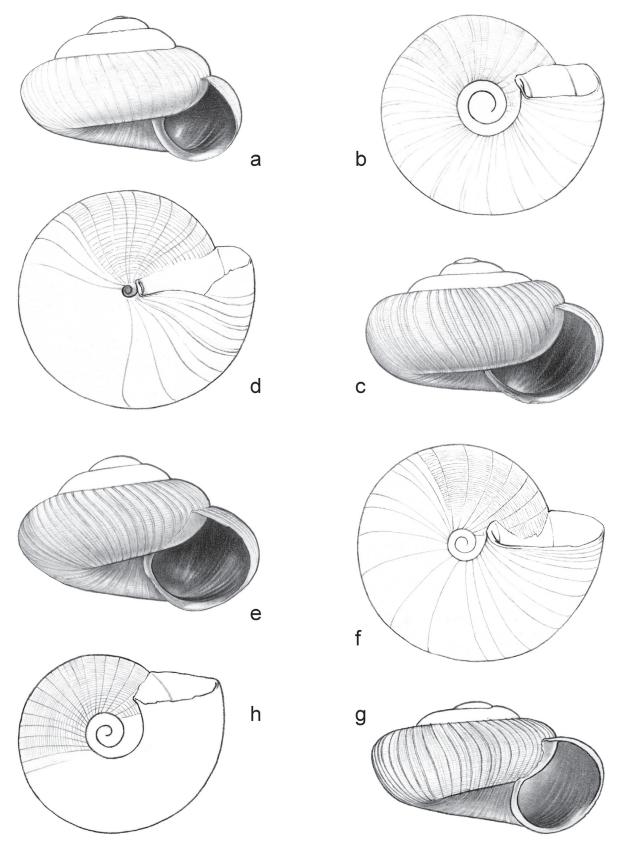


Fig. 155, a–b. *Paralaoma albella* Vermeulen & Liew, new species, a. Frontal view, shell 0.7 mm high, b. Umbilical view; c–d. *Paralaoma angusta* Vermeulen, Liew & Schilthuizen, 2015, c. Frontal view, shell 1.1 mm high, d. Umbilical view; e–f. *Paralaoma gracilitesta* (Van Benthem Jutting, 1959), e. Frontal view, shell 0.8 mm high, f. Umbilical view; g–h. *Paralaoma servilis* (Shuttleworth, 1852), g. Frontal view, shell 0.9 mm high, h. Umbilical view.

shell width; number of whorls up to 3 3/4; height aperture up to 0.75 mm; width aperture up to 0.9 mm.

Distribution in Sabah. Widespread but rare: Hills near Kota Kinabalu, Batu Timbang. Elevation range: 100–700 m. Secondary forest on sandstone/shale bedrock. Also in Sarawak. Endemic to Borneo.

Paralaoma gracilitesta (Van Benthem Jutting, 1959)

(fig.155e–f, map 34c)

Liew et al. 2010: Online Supporting Information, Appendix S1. – *Pyramidula gracilitesta* Van Benthem Jutting 1959: 124. – Type from Indonesia, Sumatra, E coast.

Paralaoma caputspinulae auct. Vermeulen & Whitten 1998: 94, 149 (partly, excluding fig.); Schilthuizen 2004: 95 (partly).

[Not Paralaoma caputspinulae (Reeve)].

Description. Shell minute, thin, slightly translucent, pale yellowish (brown). Surface shiny. Spire low-conical. Whorls not or hardly shouldered just below the suture, narrowly rounded to obtusely angular at the periphery. Sculpture. Protoconch without radial riblets, with fine, rather densely placed spiral threads. Teleoconch. Radial sculpture: Usually rather distinct, well-spaced radial ribs with a periostracal crest, which gradually disappear on the lower surface; in between these fine, densely placed, low secondary riblets above the periphery. Spiral sculpture: Spiral threads, as fine and as densely placed as the secondary radial riblets, above and below the periphery. Umbilicus rather narrow. Aperture broadly crescent-shaped, peristome not thickened, not spreading. Dimensions. Height up to 0.95 mm; width up to 1.25 mm; diameter of the first three whorls 0.35–0.45 mm, 0.65–0.75 mm, 0.95–1.15 mm respectively; umbilicus 10–20 % of the shell width; number of whorls up to 3 3/4; height aperture up to 0.45 mm; width aperture up to 0.6 mm.

Distribution in Sabah. Highlands: Mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 900–3300 m. In primary forest, secondary forest, on limestone, sandstone/shale and granodiorite bedrock. Distribution elsewhere: Indonesia (Sumatra, Java, Bali).

Paralaoma servilis (Shuttleworth, 1852)

(fig. 155g–h, map 34d)

Wallbrink et al. 2001: 89; Liew et al. 2010: Online Supporting Information, Appendix S1. – *Helix servilis* Shuttleworth 1852b: 140; Reeve 1852 (1851–1854): Pl. 143, fig. 915. – *Helix (Patula) servilis* (Shuttleworth) Pfeiffer 1855b: 126. – *Patula servilis* (Shuttleworth) Pfeiffer 1872 (1870–1876): 63. – *Patula (Patulastra) servilis* (Shuttleworth) Pfeiffer & Clessin 1881: 88. – Type from Spain, Canary Islands.

Helix caputspinulae Reeve 1852 (1851–1854): Pl. 133, fig. 818. – *Paralaoma caputspinulae* (Reeve) Vermeulen & Whitten 1998: 94, 149 (partly, including figure); Schilthuizen 2004: 95. – Type from New Zealand.

Patula javana Von Möllendorff 1897: 65. – Pyramidula humilis javana (Von Möllendorff) Rensch 1932: 124. – Pyramidula javana (Von Möllendorff) Van Benthem Jutting 1952: 352. – Type from Indonesia, Java.

[Not *Paralaoma caputspinulae* auct. Vermeulen & Whitten 1998: 94, 149 (partly, excluding fig.); Schilthuizen 2004: 95 (partly); = *Paralaoma albella* Vermeulen & Liew (partly) and *P. gracilitesta* (Van Benthem Jutting) (partly)].

Cross diagnosis. Differs from *Paralaoma gracilitesta* by being larger, by the more rapidly expanding whorls (diameter of the first three whorls 0.40–0.50 mm, 0.90–0.95 mm, 1.45–1.70 mm respectively, versus 0.35–0.45 mm, 0.65–0.75 mm, 0.95–1.15 mm), and usually by the wider umbilicus (20–27 % of the shell width, versus10–20 %).

Description. Shell minute, thin, slightly translucent, yellowish. Surface shiny. Spire low-conical to lenticular. Whorls not or hardly shouldered just below the suture, narrowly rounded at the periphery. Sculpture. Protoconch without radial riblets, with rather fine, rather densely placed spiral threads. Teleoconch. Radial sculpture: Distinct, well-spaced radial ribs, often with a periostracal crest, which gradually disappear on the lower surface; in between these fine, densely placed, low secondary riblets above the periphery. Spiral sculpture: Spiral threads, as fine and as densely placed as the secondary radial riblets, above and below the periphery, sometimes grading into somewhat coarser grooves near the umbilicus. Aperture approx. reniform, peristome not thickened, not spreading. Umbilicus rather narrow. Dimensions. Height up to 1.25 mm; width up to 2.3 mm; diameter of the first three whorls 0.40–0.50 mm, 0.90–0.95 mm, 1.45–1.70 mm respectively; umbilicus 20–27 % of the shell width; number of whorls up to 3 5/8; height aperture up to 0.9 mm; width aperture up to 1.0 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation: c. 2000 m. Found in a damp roadside with grass and shrubs. Distribution elsewhere: Widespread, W Europe and Africa, Asia, Australia including Tasmania, and New Zealand.

Variability. The spire can be higher conical than in the illustrated specimen.

Family RYSSOTIDAE Schileyko 2003

Diagnosis for the Sabah species. Snails. Shell with up to 4 1/8–4 3/4 slowly expanding whorls. Shell sinistral, very large, wider than high; spire low-conical with slightly convex sides; last whorl obtusely angular. Teleoconch sculpture: growth lines and uneven, oblique, wavy sculpture above the periphery, spiral sculpture inconspicuous, below the periphery only. Aperture without teeth. Peristome on the palatal side thickened, not spreading. Umbilicus closed. Dimensions: 33–67 mm high, 60–85 mm wide.

Genus Exrhysota H B Baker, 1941

Notes. 1. *Dyakia* (Dyakiidae) is smaller, and with a sharper keel around the periphery. The Sabah species of *Dyakia* do not have a thickened peristome.

2. The shell of *Exrhysota brookei* strongly resembles Indochinese *Bertia* and has often been included in that genus. Sutcharit et al. (2019a) list anatomical differences between *Exrhysota* and *Bertia* and place the latter in Dyakiidae. Schileyko (2003) places *Exrhysota* in Ryssotidae, Bouchet et al. (2017) in Chronidae. Shell shape and size, distinct from local Chronidae, lead us to follow Schileyko.

Exrhysota brookei (A Adams & Reeve, 1850)

(fig. 156a–d, map 34e)

Schileyko 2003: 1346; Marzuki et al. 2021: 94. – *Helix brookei* A Adams & Reeve 1850 (1848–1850): 60; Metcalfe 1852 (1851): 70; Reeve 1852 (1851–1854): Pl. 73, fig. 377; Pfeiffer 1853: 52; 1853 (1853–1860): 350. – *Nanina (Ryssota) brookei* (A Adams & Reeve) Pfeiffer 1855b: 121 ('*Rhyssota*'); Bock 1881: 633 ('*Rhyssota*'). – *Ryssota brookei* (A Adams & Reeve) Wallace 1865: 407; Godwin-Austen 1891: 27 ('*Rhysota*'); Schepman 1896: 153; Wiegmann 1898: 291 ('*Rhysota*'); Von Martens 1908: 260 ('*Rhysota*'). – *Nanina brookei* (A Adams & Reeve) Von Martens 1867: 238; Issel 1874: 397; Tenison Woods 1888: 1024; Aldrich 1889: 24. – *Nanina (Ariophanta) brookei* (A Adams & Reeve) Pfeiffer & Clessin 1881: 55; Von Martens 1908: 284. – *Bertia (Exrhysota) brookei* (A Adams & Reeve) Baker 1941: 321; Solem 1964: 26. – *Bertia brookei* (A Adams & Reeve) Schilthuizen & Rutjes 2001: 421; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Uchida et al. 2013: 53, 55. – Type from 'Borneo'.

Helix gigas Pfeiffer 1850b: 81. Type from Indonesia, 'Sumatra' (this later implicitly corrected under *Helix brookei* in Pfeiffer 1853: 52).

Cross diagnosis. The largest low-conical land snail species in Borneo.

Description. Shell very large, rather solid, opaque, ochre to very dark (reddish) brown above, just above the periphery usually with a narrow band of pale brown or white, just below the periphery a wider band of darker brown, grading to a paler brown or white towards the umbilical region. Surface somewhat silky above, shiny below. Spire low-conical with slightly convex sides, apex obtuse. Whorls moderately convex, the outer whorls slightly shouldered below the suture, last whorl obtusely angular at the periphery. Sculpture. Protoconch with radial riblets which fuse to coarser wrinkles or to a row of indentations below the suture; spiral sculpture subordinate to the radial sculpture, widely spaced, low, threads. Teleoconch above the periphery with distinct, uneven growth lines and low riblets; with coarse, low undulations perpendicular to these; next to this with a granulation much finer than the radial riblets; below the periphery with growth lines and riblets as above, as well as (traces of) a very fine spiral wrinkling. Aperture white inside. Peristome thickened but not spreading in adult shells, parietal side with a thick glazing. Umbilicus closed. Dimensions. Height 33.5–67.0 mm; width 60–85 mm, ratio height/ width 0.52–0.79; diameters of the first 3 whorls 4.8–6.2 mm, 13.0–14.5 mm, 28.5–31.5 mm respectively; number of whorls 4 1/8–4 3/4; height aperture 18–39 mm; width aperture 31–51 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1200 m. Primary and secondary forest on bedrock of all types, sometimes in more degraded vegetation. Also in Brunei, Sarawak, Kalimantan. Endemic to Borneo.

Note. Extensive anatomical description in Wiegmann (1898).

Family **TROCHOMORPHIDAE** Von Möllendorff, 1890

Diagnosis for the Sabah species. Snails. Shell with up to 5 1/8–8 3/8 slowly expanding whorls. Shell dextral, small to medium-sized, approx. as high as wide or wider than high; spire conical (with convex sides) to (depressed) lenticular; last whorl acutely keeled at the periphery. Teleoconch sculpture: Radial sculpture consisting of growth

lines locally raised to riblets, or of fine, dense radial riblets (an inconspicuous, oblique, wavy sculpture above the periphery in *Geotrochus spilokeiria*); spiral sculpture consisting of fine and/or distinct threads; next to this a minute granulation present in some species. Aperture without teeth. Peristome on the palatal side thickened or not, spreading or not. Umbilicus closed, or open, narrow to wide. Dimensions: Adults 5.5–10.4 mm high, 9.3–24.5 mm wide.

KEY TO THE GENERA (SABAH SPECIES ONLY)

1 – Umbilicus open, wide

Genus Videna

1 – Umbilicus closed

Genus Geotrochus

Genus Geotrochus Van Hasselt, 1823

(Incl. Trochomorpha auct.)

Diagnosis for the Sabah species. Shell rather small to medium-sized, dextral. Periphery keeled. Sculpture. Protoconch smooth. Teleoconch. Spiral sculpture: Thin threads, some close to the periphery usually slightly coarser where they cross the radial sculpture. Umbilicus closed.

Note. Chang & Liew (2021) present a molecular phylogeny of the Sabah species attributed to *Geotrochus* and *Trochomorpha* in Vermeulen et al. (2015) and demonstrate that the two genera cannot be maintained within the Sabah context. The scope of their paper is regional and therefore does not allow a meaningful alternative taxonomy apart from including the Sabah *Trochomorpha* species in *Geotrochus*.

KEY TO THE GROUPS

- 1 Last whorl with spiral sculpture of distinct threads which are highest or nodular where they cross the radial sculpture, lower or absent elsewhere Group 5
- 1 Last whorl with spiral sculpture of thin threads, some close to the periphery usually slightly coarser but not higher where they cross the radial sculpture
 - 2 Suture in the outer whorls of adult shells slightly below the periphery of the whorl above **Group 1**
 - 2 Suture between the whorls coinciding with the periphery of the whorl above
 - 3 Shell 13.5–24.5 mm wide in adult specimens

Group 4

- 3 Shell 10.0–12.5 mm wide in adult specimens
 - 4 Spire (moderately) low-conical with approx. straight sides

Group 2

4 – Spire (elongated-)conical with convex or concave sides

Group 3

Group 1

Geotrochus meristotrochus Vermeulen, Liew & Schilthuizen, 2015 (fig. 157a-b, 161a, map 34f)

Vermeulen et al. 2015: 131. – Type from Malaysia, Sabah, Interior Prov., Sapulut valley, Batu Punggul. *Geotrochus meristotrochus*, unavailable name, Clements et al. 2008: 2762.

Cross diagnosis. Shell less wide than *Geotrochus subscalaris* (shell width of adult specimens with thickened peristome 9.3–10.8 mm versus 11.0–13.0 mm; width aperture of adult specimens 4.8–5.5 mm versus 6.0–7.2 mm). Usually, the ratio height/width is also higher than in *G. subscalaris* (0.59–0.67 versus 0.52–0.59).

Description. Shell rather small, rather thin, about opaque, yellowish to pale brown. Surface with a silky luster. Spire moderately low-conical with straight to slightly convex sides; apex slightly protruding or not. Whorls: Apical whorls moderately convex, outer slightly convex; suture impressed, between the outer 4–5 whorls slightly below the periphery; last whorl acutely angular, slightly compressed at the periphery, rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery some growth lines, locally grading into inconspicuous riblets; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, slightly pinched peripheral keel; start of fifth whorl above the periphery with 6–9 thin, widely spaced spiral threads including 1–2 distinct ones close to the periphery, as well as 4–8 inconspicuous ones above these; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height 6.0–7.0 mm; width 9.3–10.8 mm; ratio height/width 0.59–0.67; diameters of the first 4 whorls 1.0–1.4 mm, 1.8–2.2 mm, 2.7–3.4 mm, 4.0–5.0 mm respectively; number of whorls 6 3/4–7 3/8, including a protoconch of 2 1/8–2 1/2 whorl; height aperture 2.8–3.5 mm; width aperture 4.8–5.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1700 m. In primary forest, secondary forest and abandoned agricultural land on limestone and sandstone/shale bedrock. Endemic to Sabah.



Fig. 156, a–d. *Exrhysota brookei* (A Adams & Reeve, 1850), a. Frontal view, shell 41 mm high, b. Umbilical view, c. Apical view; d. Animal devouring a mushroom.

Geotrochus subscalaris Vermeulen, Liew & Schilthuizen, 2015

(fig. 157c, 161b, map 35a)

Vermeulen et al. 2015: 129; Marzuki et al. 2021: 92. – Type from Malaysia, Sabah, Sandakan Prov., Kinabatangan river valley, Batu Pangi.

Geotrochus heraclea auct. Solem 1964: 27.

Geotrochus bongaoensis auct. Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41.

[Not Trochonanina heraclea E A Smith].

[Not *Trochonanina bongaoensis* E A Smith].

Description. Shell rather small, rather thin, about opaque, yellowish to pale brown. Surface with a silky luster. Spire moderately low-conical with slightly concave to slightly convex sides; apex slightly to moderately protruding. Whorls: Apical whorls moderately convex, outer approx. flat to slightly convex; suture impressed, between the outer 4–5 whorls slightly below the periphery; last whorl acutely angular, compressed at the periphery, rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery some growth lines, locally grading into inconspicuous riblets; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, pinched peripheral keel; start of fifth whorl above the periphery with 6–10 thin, widely spaced spiral threads, usually including 1–2 (slightly) more distinct ones close to the periphery, as well as 5–10 inconspicuous above these; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height 6.2–7.3 mm; width 11.0–13.0 mm, ratio height/width 0.52–0.59; diameters of the first 4 whorls 1.1–1.4 mm, 1.9–2.4 mm, 2.7–3.6 mm, 4.0–4.8 mm respectively; number of whorls 6 1/4–8, including a protoconch of 2 1/8–2 1/4 whorls; height aperture 3.2–4.0 mm; width aperture 6.0–7.2 mm.

Distribution in Sabah. Widespread and common in E; rare elsewhere: Sukau. Elevation range: 0–1000 m. In primary and secondary forest and more degraded vegetation on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Group 2

Geotrochus kitteli Vermeulen, Liew & Schilthuizen, 2015

(fig. 157d, map 35a)

Vermeulen et al. 2015: 127. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., Headquarters area, Silau Silau.

Geotrochus sp. 1 Liew et al. 2010: Online Supporting Information, Appendix S1; partly. *Geotrochus* sp. 2 Liew et al. 2010: Online Supporting Information, Appendix S1; partly.

Cross diagnosis. Differs from *Geotrochus whiteheadi* by the higher ratio height/width (c. 0.55 versus 0.44–0.48), and by the more distinct growth lines above the periphery, which give the shell surface a rough appearance. It also resembles *Geotrochus rhysa* (Group 5) but differs by its somewhat pinched peripheral keel and the not-nodular spiral sculpture above the periphery.

Description. Shell rather small, rather thin, about opaque, yellowish brown, whorls slightly darker brown towards the periphery. Surface dull or slightly shiny above the periphery, shiny below. Spire moderately low-conical with approx. straight sides; apex not protruding. Whorls: Apical whorls moderately convex, outer slightly convex, slightly shouldered; suture somewhat impressed, coinciding with the periphery; last whorl acutely angular, slightly compressed at the periphery, rounded below the periphery. Sculpture. Protoconch smooth (see remark, below). Teleoconch. Radial sculpture: Above the periphery rather distinct growth lines, raised at uneven intervals and wrinkling the shell surface, most conspicuously so below the suture, giving the shell surface a somewhat rough appearance; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, somewhat pinched peripheral keel; start of fifth whorl above the periphery with c. 15 thin, moderately spaced spiral threads, including 1–2 slightly more distinct ones close to the periphery, as well as 13–14 inconspicuous above these; no spiral sculpture below the periphery. Aperture approx. crescent-shaped. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height c. 5.5 mm; width c. 10 mm; ratio height/width c. 0.55; diameters of the first 4 whorls c. 1.2 mm, c. 2.2 mm, c. 3.3 mm, c. 4.8 mm respectively; number of whorls c. 6 3/8, including a protoconch of c. 2 1/8 whorls; height aperture c. 3.5 mm; width aperture c. 5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 1700–2400 m. In mixed montane forest on sandstone/shale bedrock. Endemic to Sabah.

Note. The available material is somewhat worn in the apical region.

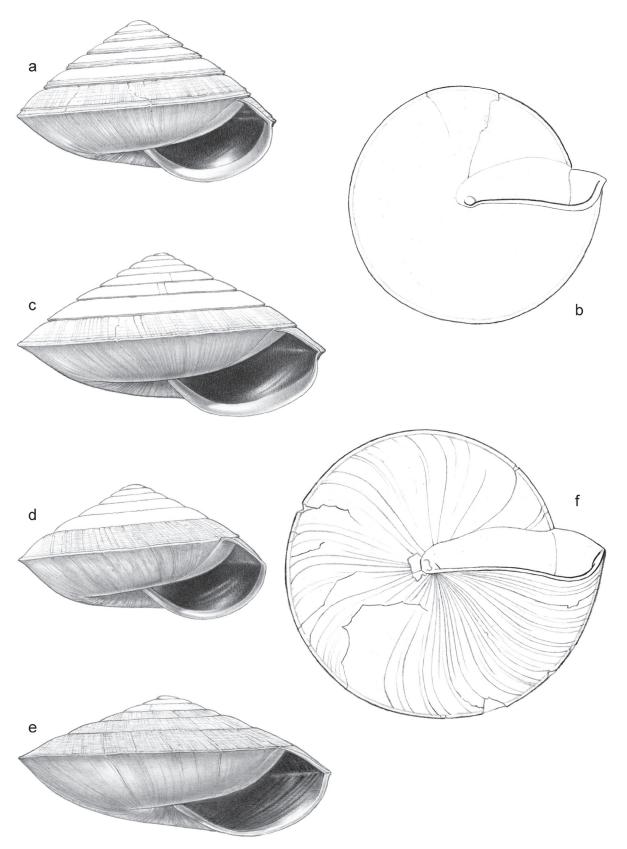


Fig. 157, a–b. *Geotrochus meristotrochus* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 7.0 mm high, b. Umbilical view; c. *Geotrochus subscalaris* Vermeulen, Liew & Schilthuizen, 2015, frontal view, shell 7.0 mm high; d. *Geotrochus kitteli* Vermeulen, Liew & Schilthuizen, 2015, frontal view, shell 5.5 mm high; e–f. *Geotrochus whiteheadi* (E A Smith, 1895), e. Frontal view, shell 5.5 mm high, f. Umbilical view.

Geotrochus whiteheadi (E A Smith, 1895)

(fig. 157e–f, map 35b)

Vermeulen 1996b: 288; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Vermeulen et al. 2015: 129; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 55. – *Trochonanina whiteheadi* Smith 1895: 106; Von Martens 1908: 260. – *Eurybasis whiteheadi* (Smith) Saul 1967: 109. – *Helix (Trochomorpha) conicoides* Metcalfe var. *parva* Smith 1887a: 132. – Type from Malaysia, Sabah, 'northern Borneo'.

Description. Shell rather small, rather thin, about opaque, pale corneous to pale brown. Surface with a silky luster above the periphery, shiny below. Spire low-conical with approx. straight sides; apex not protruding. Whorls: Apical whorls moderately convex, outer slightly convex, slightly shouldered; suture impressed in the inner whorls, hardly so in the outer, coinciding with the periphery; last whorl acutely angular, (slightly) compressed at the periphery, moderately rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery growth lines, slightly raised locally; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, somewhat pinched peripheral keel; start of fifth whorl above the periphery with c. 15 thin, moderately spaced spiral threads, including 1–2 slightly more distinct ones close to the periphery, as well as 13–14 inconspicuous above these; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height 5.5–6.0 mm; width 12.3–12.5 mm; ratio height/width 0.44–0.48; diameters of the first 4 whorls 1.2–1.4 mm, 2.1–2.4 mm, 3.4–3.8 mm, 5.2–5.8 mm respectively; number of whorls 6 1/4–6 3/8, including a protoconch of 2 1/8–2 1/4 whorls; height aperture 3.3–3.5 mm; width aperture c. 6.5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon, mount Kinabalu. Elevation range: 700–2100 m. In mixed montane forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Group 3

Geotrochus scolops Vermeulen, Liew & Schilthuizen 2015

(fig. 158a–b, map 35a)

Vermeulen et al. 2015: 126. - Type from Malaysia, Sabah, Tawau Prov., Tawau Hills N.P.

Cross diagnosis. Uniquely identified among Sabah Geotrochus by the elongated-conical shell with concave sides.

Description. Shell medium-sized, rather thin, about opaque, brown, above the periphery with a very fine, slightly paler spiral striation. Surface slightly shiny above the periphery, glossy below. Spire elongated-conical with concave sides; apex protruding. Whorls: Apical whorls moderately convex, other whorls slightly convex, slightly shouldered, last whorl almost flat; suture impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, slightly compressed at the periphery, slightly rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery growth lines, slightly raised locally; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, somewhat pinched peripheral keel; start of fifth whorl above the periphery with c. 3 thin, low, widely spaced spiral threads with an unevenly incised crest, including 1 slightly more distinct close to the periphery, as well as 2 inconspicuous above these (penultimate whorl with c. 8 such threads, of which 3–4 slightly more distinct); no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome slightly thickened, but not spreading except on the columellar side. Umbilicus closed. Dimensions. Height c. 10.4 mm; width c. 12.5 mm; ratio height/width 0.83–0.84; diameters of the first 4 whorls c. 1.1 mm, c. 1.7 mm, c. 2.2 mm, c. 3.0 mm respectively; number of whorls c. 8 3/8, including a protoconch of c. 2 whorls; height aperture c. 3 mm; width aperture c. 6.5 mm.

Distribution in Sabah. Tawau hills only. Elevation range: 700–800 m. In (disturbed) primary forest on sand-stone/shale and volcanic bedrock. Endemic to Sabah.

Geotrochus spilokeiria Vermeulen, Liew & Schilthuizen, 2015

(fig. 158c–d, map 35b)

Vermeulen et al. 2015: 125. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., Ulu Kimanis, along Keningau-Kimanis road.

Trochomorpha 'sp. nov. 2' Schilthuizen 2004: 95.

Cross diagnosis. Uniquely identified among Sabah *Geotrochus* by the brown, grey and white mottled shell with convex sides and rapidly expanding whorls. The pattern of low, vaguely outlined spiral ridges and similar rows of oblique indentations are also characteristic.

Description. Shell medium-sized, rather thin, opaque, above the periphery greyish with a somewhat vaguely outlined brown band just above the peripheral keel, and with an uneven pattern of white stains and spots which

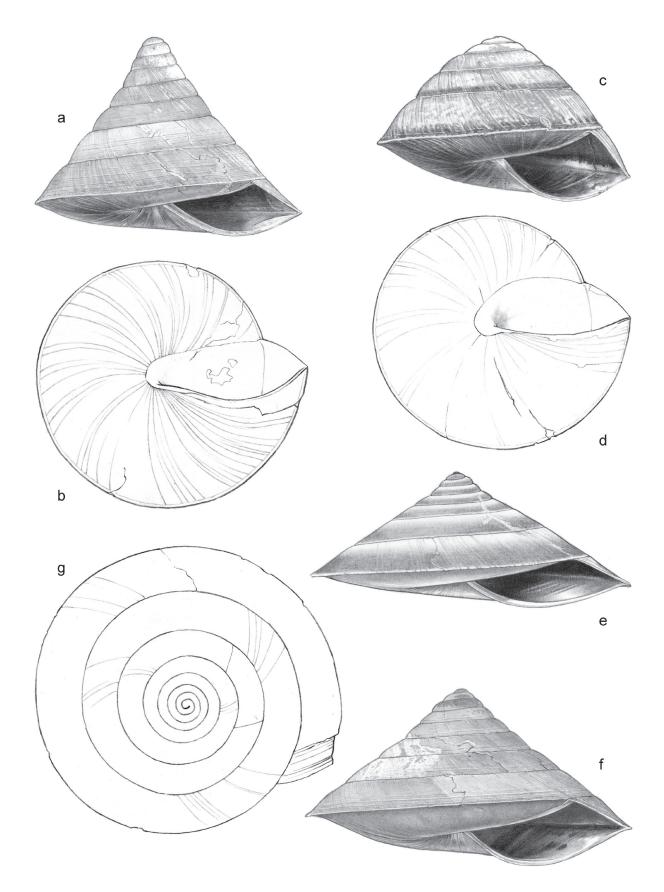


Fig. 158, a–b. *Geotrochus scolops* Vermeulen, Liew & Schilthuizen, 2015, a. Frontal view, shell 10 mm high, b. Umbilical view; c–d. *Geotrochus spilokeiria* Vermeulen, Liew & Schilthuizen, 2015, c. Frontal view, shell 8.5 mm high, d. Umbilical view; e–g. *Geotrochus conicoides* (Metcalfe, 1852), frontal views, e. Shell 11 mm high, f. Shell 8.5 mm high; g. Apical view.

approx. follow the radial and spiral sculpture, periphery white, below the periphery dark brown, grading to white towards the periphery. Surface shiny above the periphery, glossy below. Spire conical with convex sides; apex not protruding. Whorls: Apical whorls moderately convex, next whorls slightly convex, slightly shouldered, outer whorl almost flat; suture somewhat impressed in the apical whorls, not so in the outer whorls, coinciding with the periphery; last whorl acutely angular, slightly compressed at the periphery, slightly rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery rather distinct growth lines, raised at uneven intervals; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a sharp, pinched peripheral keel; above and close to this keel 1 thin, low, sharply outlined spiral thread; above this 3–4 very low and wide, vaguely outlined ridges locally visible in tangential light; next to this radial and spiral sculpture oblique rows of very shallow, vaguely outlined indentations are locally visible; below the periphery locally with traces of a fine, shallow, vaguely outlined spiral striation. Aperture obtusely trapezoid. Peristome not thickened, nor spreading except on the columellar side (see notes below). Umbilicus closed. Dimensions. Height c. 8.5 mm; width c. 12.5 mm; ratio height/width c. 0.68; diameters of the first 4 whorls c. 1.5 mm, c. 2.7 mm, c. 4.6 mm, c. 7.0 mm respectively; number of whorls c. 5 5/8, including a protoconch of c. 1 5/8 whorls; height aperture c. 3.5 mm; width aperture c. 7.0 mm.

Distribution in Sabah. Highlands: Crocker range only. Elevation range: 1200–1300 m. In (disturbed) primary forest on sandstone/shale bedrock. Endemic to Sabah.

Note. The only shell available is possibly sub-adult.

Group 4

Geotrochus conicoides (Metcalfe, 1852)

(fig. 158e–g, map 35b)

Van Benthem Jutting 1959: 143; Schilthuizen & Rutjes 2001: 420; Vermeulen et al. 2015: 123; Phung et al. 2017: 94; Marzuki et al. 2021: 91. – Helix conicoides Metcalfe 1852 (1851): 71; Von Martens 1867: 256. – Trochomorpha conicoides (Metcalfe) Wallace 1865: 407; Issel 1874: 404. – Nigritella conicoides (Metcalfe) Godwin-Austen 1891: 42. – Dendrotrochus conicoides (Metcalfe) Kobelt 1897: 50; Wiegmann 1898: 371. – Trochonanina conicoides (Metcalfe) Pfeiffer & Clessin 1881: 57; Tenison Woods 1888: 1026; Dohrn 1889: 59; Schepman 1896: 156; Von Martens 1908: 260, 284. – Eurybasis conicoides (Metcalfe) Van Benthem Jutting 1941: 23. – Type from 'Borneo'.

Cross diagnosis. Generally characterized by the conical spire, but low-conical specimens occur. In shape these approach the other species in Group 4, particularly *Geotrochus labuanensis*, but have a more distinctly protruding apex and more distinctly concave sides. Also, relative to the shell height, the peripheral keel is positioned closer to the base of the shell (peripheral keel of the last whorl at 0.57–0.66 of the shell height, measured from the apex, versus 0.33–0.54 of the shell height), and the lower surface of the shell is often rather distinctly concave towards the periphery.

Description. Shell medium-sized, rather thin, opaque, uniformly pale to dark brown (some material from Sarawak a paler brown just below the suture). Surface approx. dull, or with a silky luster above the periphery, shiny below. Spire (low-)conical with almost flat to distinctly concave sides, apex slightly to distinctly protruding. Whorls: Apical whorls moderately convex, next whorls approx. flat to slightly convex, outer whorls often flat; suture impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, (distinctly) compressed at the periphery, slightly to rather distinctly concave just below the periphery, slightly to moderately convex towards the umbilical region. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above and below the periphery inconspicuous growth lines, somewhat raised locally. Spiral sculpture: Last whorl with a sharp, distinctly pinched peripheral ridge; start of fifth whorl above the periphery with 5-17 rather densely placed to somewhat spaced, low and thin spiral threads, the 2-5 threads close to the periphery usually slightly more distinct, the others very inconspicuous or (almost) absent; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height 7.7-10.0 mm; width 16.0-19.8 mm; ratio height/width 0.42-0.53; peripheral keel of the last whorl at 0.57-0.66 of the shell height, measured from the apex; diameters of the first 4 whorls 1.3-1.5 mm, 2.0-2.5 mm, 2.5-4.0 mm, 4.2-5.6 mm respectively; number of whorls 7–8, including a protoconch of 1 7/8–2 1/2 whorls; height aperture 2.8–3.8 mm; width aperture 8–9.5 mm.

Distribution in Sabah. Widespread but rare: Pulau Tiga Park, W Coast Islands, Tawau hills. Elevation range: 0–400 m. In primary and old secondary forest on sandstone/shale and volcanic bedrock, living on decaying wood. Also in Sarawak. Distribution elsewhere: Indonesia (Sumatra), Philippines (Palawan).

Note. Extensive anatomical description in Wiegmann (1898).

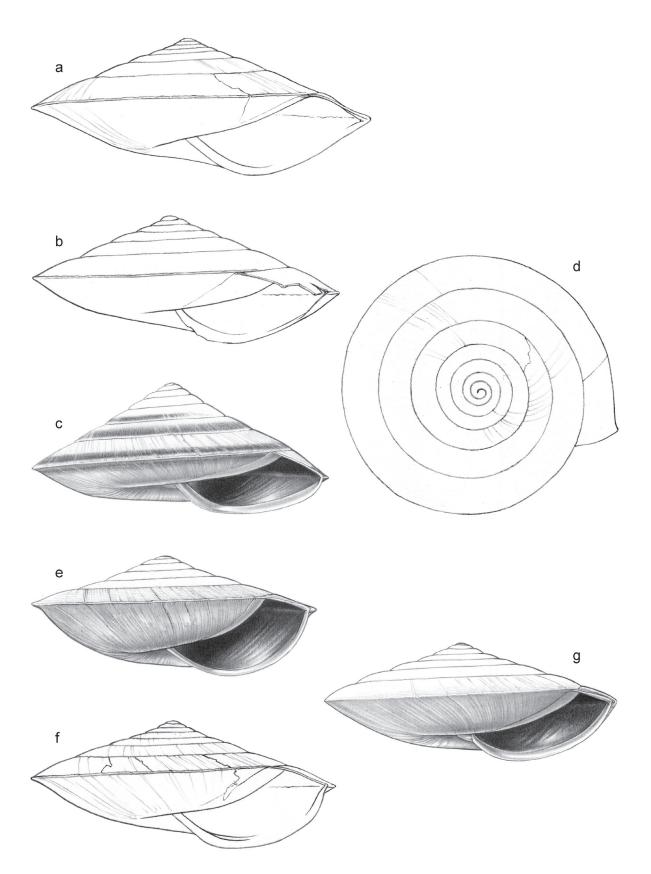


Fig. 159, a–b. *Geotrochus kinabaluensis* (E A Smith, 1895), frontal views, a. Shell 10 mm high, b. Shell 7.4 mm high (peristome damaged); c–d. *Geotrochus labuanensis* (L Pfeiffer, 1864), c. Frontal view, shell 7 mm high, d. Apical view; e–f. *Geotrochus oedobasis* Vermeulen, Liew & Schilthuizen, 2015, frontal views, e. Shell 6 mm high, f. Shell 8.5 mm high; g. *Geotrochus paraguensis* (E A Smith, 1893), frontal view, shell 7 mm high.

Geotrochus kinabaluensis (E A Smith, 1895)

(fig. 159a-b, 161c, map 35c)

Vermeulen 1996b: 288; Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 121. – *Trochonanina kinabaluensis* Smith 1895: 105. – *Trochomorpha kinabaluensis* Von Martens 1908: 261. – *Eurybasis kinabaluensis* (Smith) Laidlaw 1937: 180. – Type from Malaysia, Sabah, mount Kinabalu.

Trochonanina kinabaluensis E A Smith var. *pallida* Smith 1895: 106. – *Geotrochus pallida* (E A Smith) Liew et al. 2010: Online Supporting Information, Appendix S1. – Type from Malaysia, Sabah, mount Kinabalu.

[Not *Geotrochus kinabaluensis* auct. Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41; = *Geotrochus labuanensis*].

Description. Shell medium-sized, rather thin, opaque, brown, sometimes a slightly paler brown just below the suture, periphery pale brown to dull white. Surface with a silky luster above the periphery, shiny below. Spire low-conical with approx. straight sides, apex not or hardly protruding. Whorls slightly convex; suture impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, moderately compressed at the periphery, slightly convex below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above and below the periphery scattered inconspicuous growth lines, locally grading into inconspicuous riblets; next to this a very fine (just visible at 40x magnification) radial wrinkling of the shell surface is locally present. Spiral sculpture: Last whorl with a sharp, slightly pinched peripheral ridge; start of fifth whorl above the periphery with 15–17 somewhat spaced, low and thin spiral threads, the 2–5 threads close to the periphery slightly more distinct, the others inconspicuous; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading, basal side most strongly curved towards the columellar side, approx. straight or slightly concave towards the periphery. Umbilicus closed. Dimensions. Height 7.4-10.0 mm; width 17.6-24.5 mm; ratio height/width 0.41-0.42; peripheral keel of the last whorl at 0.40-0.45 of the shell height, measured from the apex; diameters of the first 4 whorls 1.5-1.6 mm, 2.4-2.6 mm, 3.4-4.6 mm, 5.8-6.5 mm respectively; number of whorls 6 1/2–6 3/4, including a protoconch of c. 2 1/8 whorls; height aperture 4.0–5.5 mm; width aperture 9.0–13.0 mm.

Distribution in Sabah. Widespread, scattered localities. Elevation range: 0–2000 m. In primary and secondary forest on sandstone/shale and granodiorite bedrock, living on decaying wood. Endemic to Sabah.

Geotrochus labuanensis (L Pfeiffer, 1864)

(fig. 159c–d, map 35d)

Solem 1964: 27; Clements et al. 2008: 2762; Vermeulen et al. 2015: 120. – *Helix labuanensis* Pfeiffer 1864 (1863): 523; 1866 (1866–1869): 304; 1868: 61. – *Trochonanina conicoides* var. *labuanensis* (L Pfeiffer) Pfeiffer & Clessin 1881: 57. – *Nanina conicoides* (Metcalfe) var. *labuanensis* (L Pfeiffer) Tryon 1886: 48. – *Trochonanina labuanensis* (L Pfeiffer) Von Martens 1908: 260. – Type from Malaysia, 'Labuan island'.

Helix vitrea Bonnet 1864: 68. – Type from 'l'Amérique du Sud'.

Eurybasis alexis auct. Saul 1967: 109.

Geotrochus kinabaluensis auct. Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41.

Geotrochus bongaoensis auct. Liew et al. 2010: Online Supporting Information, Appendix S1.

[Not Trochonanina alexis Smith 1895: 100, 105; = Geotrochus paraguensis (E A Smith)].

[Not Geotrochus kinabaluensis E A Smith].

[Not Trochonanina bongaoensis E A Smith].

Cross diagnosis. Differs from Geotrochus kinabaluensis by the presence of a peripheral color band (not always present), and a smaller aperture. The spiral sculpture above the periphery is often more widely spaced, and more unequal, with a few stronger threads close to the periphery and very inconspicuous ones, if any, elsewhere. The position of the peripheral keel relative to the shell height is intermediate between G. kinabaluensis and G. oedobasis.

Description. Shell medium-sized, rather thin, opaque, creamy white, greyish, or very pale yellowish brown, periphery white, with a narrow, rather vaguely outlined, pale to dark (ochre-)brown band immediately above it, and often a second, similar band immediately below it. Surface shiny. Spire low-conical with approx. straight sides, apex not or hardly protruding. Whorls: Inner whorls moderately convex, outer whorls flat to slightly convex; suture impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, slightly compressed at the periphery, slightly convex below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above and below the periphery scattered inconspicuous growth lines, locally grading into inconspicuous riblets. Spiral sculpture: Last whorl with a sharp, slightly pinched peripheral ridge; start of fifth whorl above the periphery with 4–25 usually well-spaced, low and thin spiral threads, the 2–5 threads close to the periphery more distinct, the others very inconspicuous or absent; no spiral sculpture below the periphery. Aperture obtusely trapezoid. Peristome thickened and spreading, basal side most strongly curved towards the columellar

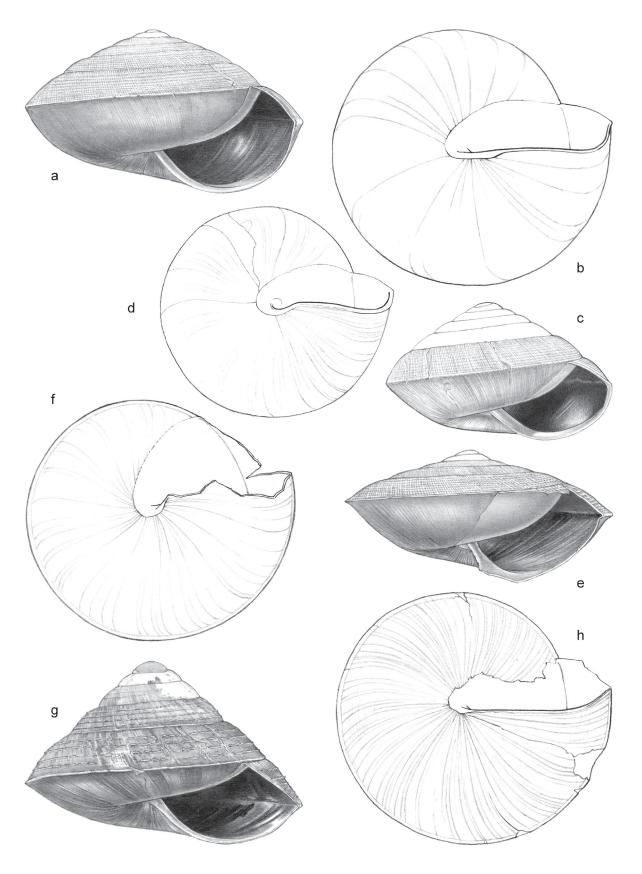


Fig. 160, a–b. *Geotrochus haptoderma* (Vermeulen, Liew & Schilthuizen, 2015), a. Frontal view, shell 10 mm high, b. Umbilical view; c–d. *Geotrochus rhysa* (Tillier & Bouchet, 1989), c. Frontal view, shell 5.8 mm high, d. Umbilical view; e–f. *Geotrochus thelecoryphe* (Vermeulen, Liew & Schilthuizen, 2015), e. Frontal view, shell 5.5 mm high, f. Umbilical view; g–h. *Geotrochus trachus* (Vermeulen, Liew & Schilthuizen, 2015), g. Frontal view, shell 8.5 mm high, h. Umbilical view.

side, and often, to a somewhat lesser extent, towards the periphery; in between only slightly curved. Umbilicus closed. Dimensions. Height 6.3–7.6 mm; width 14.5–17.8 mm; ratio height/width 0.39–0.45; peripheral keel of the last whorl at 0.44–0.54 of the shell height, measured from the apex; diameters of the first 4 whorls 1.3–1.6 mm, 2.2–2.7 mm, 3.6–4.4 mm, 5.2–7.0 mm respectively; number of whorls 6 1/8–6 7/8, including a protoconch of 2 1/8–2 1/2 whorls; height aperture 3.0–3.6 mm; width aperture 7.4–9.2 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–1500 m. In primary and secondary forest on limestone and sandstone/shale bedrock, living on decaying wood. Endemic to Sabah.

Note. Geotrochus labuanensis is a lowland species, contrary to G. kinabaluensis and G. oedobasis.

Geotrochus oedobasis Vermeulen, Liew & Schilthuizen, 2015

(fig. 159e–f, 161d, map 35e)

Vermeulen et al. 2015: 122. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., Headquarters area. *Geotrochus* sp. (V 1191) Vermeulen 1996b: 288.

Cross diagnosis. Differs from *Geotrochus kinabaluensis* and *G. labuanensis* by the evenly rounded basal peristome. Relative to the shell height, the peripheral keel is positioned closer to the apex of the shell than in the other two species. It makes the lower side of the shell appear more convex, and the upper side flatter.

Description. Shell medium-sized, rather thin, opaque, uniformly somewhat pale brown, periphery paler brown. Surface with a silky luster above the periphery, shiny below. Spire low-conical with approx. straight or slightly concave sides, apex not or hardly protruding. Whorls: Apical whorls slightly convex, other whorls approx. flat; suture somewhat impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, (moderately) compressed at the periphery, moderately to distinctly convex below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above and below the periphery scattered inconspicuous growth lines, locally grading into inconspicuous riblets; next to this a very fine (just visible at 40x magnification) radial wrinkling of the shell surface is locally present. Spiral sculpture: Last whorl with a sharp, slightly pinched peripheral ridge; start of fifth whorl above the periphery with 19-23 somewhat spaced, low and thin spiral threads, the 2-5 threads close to the periphery slightly more distinct, the others inconspicuous; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading, basal side approx. evenly rounded from the columellar side to the periphery. Umbilicus closed. Dimensions. Height 6.0-8.5 mm; width 13.5-18.0 mm; ratio height/width 0.39-0.45; peripheral keel of the last whorl at 0.33-0.40 of the shell height, measured from the apex; diameters of the first 4 whorls 1.3-1.4 mm, 2.2-2.3 mm, 3.7-4.0 mm, 5.9-6.4 mm respectively; number of whorls 6-7 1/8, including a protoconch of 2-2 1/8 whorls; height aperture 3.5-5.2 mm; width aperture 7.0-10.0 mm.

Distribution in Sabah. Scattered localities in W: Mount Tambuyukon, mount Kinabalu, Crocker range, Trus Madi range. Elevation range: 200–2300 m. In forest on sandstone/shale and limestone bedrock, also found in grassy roadside with forest nearby. Endemic to Sabah.

Geotrochus paraguensis (E A Smith, 1893)

(fig. 159g, map 35e)

Vermeulen et al. 2015: 118; Foon et al. 2018: 96. – *Trochonanina paraguensis* Smith 1893a: 349. – Type from Philippines, 'Palawan'.

Trochonanina alexis Smith 1895: 100, 105; Von Martens 1908: 260. – Type from Malaysia, Sabah, Kudat Prov., Banggi island.

Geotrochus bongaoensis auct. Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96.

[Not Eurybasis alexis auct. Saul 1967: 109; = Geotrochus labuanensis (L Pfeiffer)].

[Not Trochonanina bongaoensis E A Smith].

Cross diagnosis. Distinct in Group 5 by a combination of characters: Spiral color bands absent, periphery not pinched, whorls and lower surface of the shell moderately convex.

Description. Shell medium-sized, rather thin, opaque, uniformly pale yellowish brown. Surface with a silky luster above the periphery, shiny below. Spire low-conical with straight to slightly convex sides; apex not protruding or only slightly so. Whorls: All whorls moderately convex; suture impressed in the inner whorls, not so in the outer, coinciding with the periphery; last whorl acutely angular, not or hardly compressed at the periphery, moderately rounded below the periphery. Sculpture. Protoconch smooth. Teleoconch. Radial sculpture: Above the periphery growth lines, raised locally or grading into inconspicuous, somewhat unevenly spaced, fine, low riblets, particularly towards the periphery; below the periphery unevenly spaced growth lines only. Spiral sculpture: Last whorl with a sharp but not pinched peripheral ridge; start of fifth whorl above the periphery with 13–17 well-spaced, very fine and thin spiral threads covering most of the whorl except a narrow strip below the suture,

at least some spiral threads close to the periphery usually slightly coarser; no spiral sculpture below the periphery. Aperture approx. obtusely trapezoid. Peristome thickened and spreading. Umbilicus closed. Dimensions. Height 6.0–8.5 mm; width 14.0–22.8 mm; ratio height/width 0.37–0.42; peripheral keel of the last whorl at 0.39–0.53 of the shell height, measured from the apex; diameters of the first 4 whorls 1.4–1.8 mm, 2.4–2.7 mm, 4.0–4.6 mm, 5.7–6.9 mm respectively; number of whorls 6 3/4–7 5/8, including a protoconch of 1 7/8–2 1/8 whorls; height aperture 3.2–5.2 mm; width aperture 8–11.6 mm.

Distribution in Sabah. Rare in N: Balambangan and Banggi islands, mount Tambuyukon. Elevation range: 0–800 m. In (dry) primary forest, coastal forest and shrub vegetation on limestone and sandstone/shale bedrock. Distribution elsewhere: Philippines (Palawan).

Group 5

(Genus Trochomorpha auct. Vermeulen et al. 2015)

Geotrochus haptoderma (Vermeulen, Liew & Schilthuizen, 2015) (fig. 160a–b, 161e, map 35f)

Trochomorpha haptoderma Vermeulen et al. 2015: 114. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., near Summit trail.

Geotrochus sp. 1 Liew et al. 2010: Online Supporting Information, Appendix S1; partly. *Geotrochus* sp. 2 Liew et al. 2010: Online Supporting Information, Appendix S1; partly.

Description. Shell medium-sized, rather thin, about opaque, yellowish brown. Surface with a silky luster above the periphery, shiny below. Spire moderately low-conical with somewhat convex sides; apex slightly protruding. Whorls: Apical whorls convex, outer slightly convex; suture moderately impressed, coinciding with the periphery; last whorl angular, hardly compressed at the periphery, rounded below the periphery. Sculpture. Protoconch with dense radial riblets except at the apex, and a spiral striation cutting into the radial riblets towards the teleoconch; transition to teleoconch sculpture gradual. Teleoconch. Radial sculpture: Above the periphery rather densely placed, approx. evenly spaced riblets; below the periphery growth lines only. Spiral sculpture: Last whorl with a peripheral thread; start of fifth whorl above the periphery with 11–14 spiral threads: 2–8 rather distinct, rather low and wide threads but with a narrow crest, which are highest or form nodes over the radial sculpture, and 5–12 similar but less conspicuous threads interspersed; no spiral sculpture below the periphery. Aperture approx. crescent-shaped. Peristome slightly thickened and slightly spreading, more distinctly so on the columellar side. Umbilicus closed. Dimensions. Height 7.4–10.0 mm; width 14.0–17.0 mm; ratio height/width 0.53–0.59; diameters of the first 4 whorls 1.7–1.9 mm, 3.0–3.3 mm, 5.0–5.5 mm, 7.5–8.2 mm respectively; number of whorls 5 1/2–6 1/8, including a protoconch of 1 7/8–2 1/4 whorls; height aperture 5.0–6.0 mm; width aperture 6.5–8.5 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 2000–3400 m. In montane and sub-alpine forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Geotrochus rhysa (Tillier & Bouchet, 1989)

(fig. 160c–d, 161f, map 36a)

Trochomorpha rhysa Tillier & Bouchet 1989 (1988): 257; Vermeulen 1996b: 289; Liew et al. 2010: Online Supporting Information, Appendix S1; Vermeulen et al. 2015: 114. – Type from Malaysia, Sabah, mount Kinabalu.

Cross diagnosis. More densely coiled than *Geotrochus haptoderma* and *G. thelecoryphe* (diameter of the 4th whorl 5.5–6.0 mm versus 7.5–8.2 mm. The sculpture above the periphery is finer, particularly the radial riblets on the protoconch, and the spiral threads on the teleoconch.

Description. Shell rather small, rather thin, about opaque, (pale) yellowish brown to pale greenish brown. Surface with a silky luster above the periphery, shiny below. Spire moderately low-conical with approx. straight sides; apex not protruding. Whorls somewhat convex, outer whorls slightly shouldered; suture impressed, coinciding with the periphery; last whorl distinctly angular but not or hardly compressed at the periphery, rounded below the periphery. Sculpture. Protoconch with dense radial riblets except at the apex; transition to teleoconch sculpture abrupt. Teleoconch. Radial sculpture: Above the periphery rather densely placed, approx. evenly spaced riblets, slightly more uneven on the last whorl and fading towards the aperture; below the periphery growth lines only. Spiral sculpture: Last whorl with a peripheral thread; start of fifth whorl above the periphery with 14–19 fine, rather low and wide spiral threads of approx. equal strength, forming nodes over the radial sculpture (less distinctly so on the earlier teleoconch whorls), threads on the last whorl dissolving in rows of granules; no spiral sculpture below the periphery. Aperture obtusely quadrangular. Peristome moderately thickened and spreading, more distinctly spreading on the columellar side. Umbilicus closed. Dimensions. Height 6.0–6.8 mm; width 10–12 mm, ratio height/width 0.57–0.62; diameters of the first 4 whorls 1.4–1.5 mm, 2.3–2.5 mm, 3.7–4.0 mm, 5.5–6.0 mm respectively; number of whorls 5 3/4–6, including a protoconch of 2 1/8–2 1/4 whorls, height aperture 3.0–3.8

mm; width aperture 5.0–6.0 mm.

Distribution in Sabah. Highlands: Mount Tambuyukon and mount Kinabalu only. Elevation range: 1600–3300 m. In montane and sub-alpine forest on sandstone/shale and granodiorite bedrock. Endemic to Sabah.

Geotrochus thelecoryphe (Vermeulen, Liew & Schilthuizen, 2015) (fig. 160e–f, 161g, map 36b)

Trochomorpha thelecoryphe Vermeulen et al. 2015: 114. – Type from Malaysia, Sabah, West Coast Prov., Kinabalu N.P., near Summit trail.

Geotrochus sp. 1 Liew et al. 2010: Online Supporting Information, Appendix S1; partly. *Geotrochus* sp. 2 Liew et al. 2010: Online Supporting Information, Appendix S1; partly.

Cross diagnosis. Differs from Geotrochus haptoderma by its flatter spire, with a more protruding apex.

Description. Shell rather small, rather thin, about opaque, yellowish brown. Surface with a silky luster above the periphery, shiny below. Spire low-conical with somewhat convex sides, apex protruding. Whorls: Apical whorls convex, outer slightly convex; suture hardly impressed, coinciding with the periphery; last whorl acutely angular and compressed at the periphery, rounded below the periphery. Sculpture. Protoconch with dense radial riblets except at the apex, and a spiral striation cutting into the radial riblets towards the teleoconch; transition to teleoconch sculpture gradual. Teleoconch. Radial sculpture: Above the periphery rather densely placed, approx. evenly spaced riblets; below the periphery growth lines only. Spiral sculpture: Last whorl with a peripheral thread; start of fifth whorl above the periphery with c. 13 spiral threads: Approx. 10 rather distinct, rather low and wide threads but with a narrow crest, which are highest over the radial sculpture, or form nodes there, and c. 3 similar but less conspicuous threads interspersed; no spiral sculpture below the periphery. Aperture obtusely trapezoid. Peristome (not present on the material available). Umbilicus closed. Dimensions. Height c. 6 mm; width c. 11 mm; ratio height/width 0.54–0.55; diameters of the first 4 whorls c. 1.7 mm, c. 2.8 mm, c. 5 mm, c. 8 mm respectively; number of whorls c. 5 1/8, including a protoconch of c. 1 7/8 whorls; height aperture c. 3.5 mm; width aperture c. 6 mm.

Distribution in Sabah. Highlands: Mount Kinabalu only. Elevation range: 1900–2700 m. In montane forest on sandstone/shale bedrock. Endemic to Sabah.

Notes. Geotrochus thelecoryphe resembles G. haptoderma except for the character mentioned in the cross diagnosis, leading to suspicions that the two names refer to a single species. In the molecular phylogeny of Chang & Liew (2021) the two are part of an unresolved polytomy. For now, we retain them as separate species because of their morphological distinctness, however minimal.

Geotrochus trachus (Vermeulen, Liew & Schilthuizen, 2015) (fig. 160g–h, 161h, map 36b)

Trochomorpha trachus Vermeulen et al. 2015: 112. – Type from Malaysia, Sabah, West Coast Prov., Crocker Range N.P., near the km 54 marker on the road Kota Kinabalu-Tambunan, Gunung Mas. *Trochomorpha* 'sp. nov. 1' Schilthuizen 2004: 95.

Cross diagnosis. Uniquely identified among the Sabah species of the family by the very coarse, at uneven intervals interrupted spiral sculpture.

Description. Shell rather small, thin, opaque, reddish brown with darker brown or white streaks following growth lines, slightly paler brown with similar darker streaks below the suture. Surface dull or slightly shiny above the periphery, glossy below. Spire conical with straight sides; apex not protruding. Whorls somewhat convex, outer whorls slightly shouldered; suture impressed, coinciding with the periphery; last whorl distinctly angular and slightly compressed at the periphery, moderately rounded below the periphery. Sculpture. Protoconch (absent in available material). Teleoconch. Radial sculpture: Above the periphery unevenly spaced growth lines, developing into locally coarse, uneven wrinkling on the outer whorls, particularly below the suture; below the periphery indistinct growth lines only. Spiral sculpture: Last whorl with a peripheral thread; start of fifth whorl above the periphery with 8–9 spiral threads: 3–4 coarse, high and rather narrow threads, with c. 5 minor threads interspersed; all threads highest and most distinct over the raised radial sculpture, low or interrupted in between, at uneven intervals, and with a somewhat erose and locally incised crest; below the periphery a few traces of densely placed, shallow spiral grooves. Aperture obtusely quadrangular. Peristome not thickened, nor spreading (see note). Umbilicus closed. Dimensions. Height c. 8.5 mm; width c. 12.5 mm, ratio height/width c. 0.66; estimated diameters of the first 4 whorls c. 1.2 mm, c. 2.3 mm, c. 4.0 mm, c. 6 mm respectively; number of whorls c. 5 3/4; height aperture c. 4 mm; width aperture c. 7 mm.

Distribution in Sabah. Highlands: Crocker range only. Elevation range: 1500–1900 m. In mixed montane forest on sandstone/shale bedrock. Endemic to Sabah.

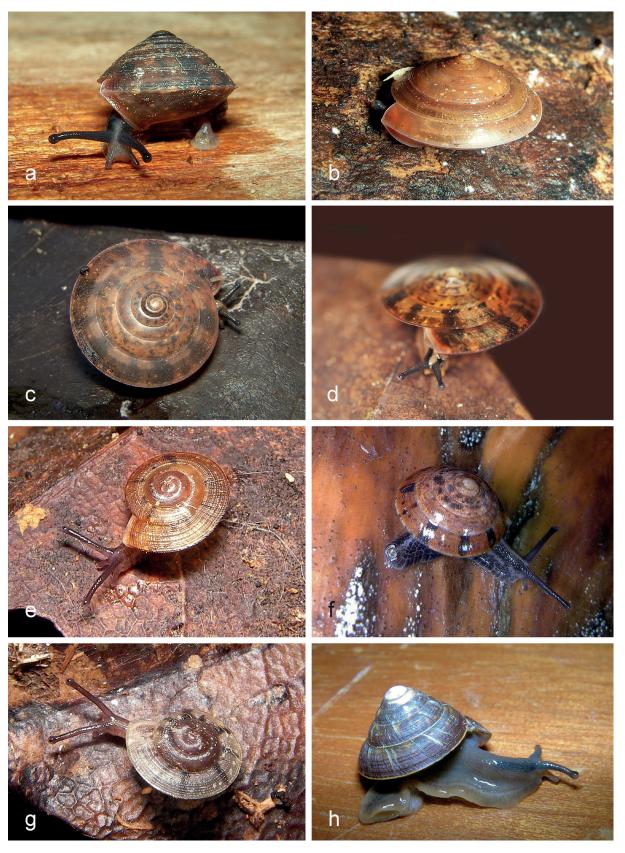


Fig. 161, a. *Geotrochus meristotrochus* Vermeulen, Liew & Schilthuizen, 2015; b. *Geotrochus subscalaris* Vermeulen, Liew & Schilthuizen, 2015; c. *Geotrochus kinabaluensis* (E A Smith, 1895); d. *Geotrochus oedobasis* Vermeulen, Liew & Schilthuizen, 2015; e. *Trochomorpha haptoderma* Vermeulen, Liew & Schilthuizen, 2015, juvenile; f. *Trochomorpha rhysa* Tillier & Bouchet, 1989; g. *Trochomorpha thelecoryphe* Vermeulen, Liew & Schilthuizen, 2015, juvenile; h. *Trochomorpha trachus* Vermeulen, Liew & Schilthuizen, 2015.

Note. The single shell available is probably sub-adult and has a damaged apex.

Genus Videna H & A Adams, 1855

Diagnosis for the Sabah species. Shell rather small to medium-sized, dextral. Periphery keeled. Sculpture. Protoconch with or without minute radial wrinkles, with or without spiral striation. Teleoconch: Spiral sculpture absent or consisting of grooves. Umbilicus open, wide.

Note. All sculpture, and particularly the microsculpture, wears off easily in old shells.

KEY TO THE GROUPS

- 1 Microsculpture present (a microscopical granulation much finer than the growth lines, just visible at 40x magnification) on the upper surface of the shell, particularly on the last whorls, towards the periphery **Group 1**
- 1 No microsculpture visible at 40x magnification

Group 2

Group 1

Videna metcalfei (L Pfeiffer, 1845)

(fig. 162a–c, 164a, map 36c)

Solem 1964: 25; Schilthuizen & Rutjes 2001: 421; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41, 42; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Liew et al. 2010: Online Supporting Information, Appendix S1; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Uchida et al. 2013: 53, 55; Phung et al. 2017: 94; Foon et al. 2018: 96. – Helix metcalfei Pfeiffer 1845: 66. – Helix (Videna) metcalfei (L Pfeiffer) Pfeiffer 1855b: 132; Bock 1881: 633. – Trochomorpha (Videna) metcalfei (L Pfeiffer) Pfeiffer & Clessin 1881: 83. – Trochomorpha metcalfei (L Pfeiffer) Von Möllendorff 1890: 210; Pilsbry 1893 (1892–1893): 121; Smith 1893a: 349; Pilsbry 1893 (1893–1895): 4; Von Martens 1908: 261, 283. – Type from Philippines, Cebu.

Description. Shell medium-sized, rather thin, opaque, pale yellowish brown to almost white, whorls usually with a narrow, rather well defined, distinct, red-brown band just above the suture. Shell shiny near the apex, otherwise silky above, approx. glossy below. Spire low-conical with slightly to distinctly convex sides and often with a rounded apex; spire only slightly raised in some shells. Whorls: First whorls moderately convex, last whorl moderately convex to flat, slightly compressed towards the periphery. Sculpture. Protoconch with minute, inconspicuous radial wrinkles towards the suture. Teleoconch above the periphery with a microscopical granulation (visible at 40x magnification), most conspicuously present on the outer whorls towards the periphery, where the granules are often aligned obliquely; with predominant, (rather) densely placed, unevenly spaced, low, rounded, raised growth lines, locally developing in radial riblets; below the periphery with a less distinct microsculpture only locally present, growth lines present, locally raised. Spiral sculpture above the periphery: Very fine, inconspicuous, densely placed, shallow, often interrupted spiral grooves on the first whorls; below the periphery spiral sculpture absent, or inconspicuous, moderately spaced, shallow grooves which disappear towards the umbilicus. Aperture somewhat obtusely quadrangular. Peristome thickened in adult shells. Umbilicus open, wide. Dimensions. Height up to 6.1 mm; width up to 17.5 mm; ratio height/width 0.29-0.40; fourth whorl 8.0-11.0 mm diam.; last whorl 32-40 % of the shell width; umbilicus up to 4.2 mm wide, which is 22–27 % of the shell width; number of whorls up to 5 1/2, height aperture up to 3.5 mm; width aperture up to 7.5 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1100 m. In (disturbed) primary forest and shrubland on limestone and serpentinite bedrock. Sometimes persistent in degraded vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Philippines.

Videna repanda (Von Möllendorff, 1890)

(fig. 162d–f, map 36d)

Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96. – *Trochomorpha repanda* Von Möllendorff 1890: 211; Pilsbry 1893 (1892–1893): 123; 1893 (1893–1895): 4; Von Möllendorff 1894: 208; Schilthuizen et al. 2011: 5. – Type from Philippines, Luzon.

Cross diagnosis. Differs from *Videna metcalfei* by the by the absence of spiral sculpture. Next to this, it differs by the much wider (covering close to half the width of the whorl or more), more vaguely outlined, brown band above the suture.

Description. Shell medium-sized, rather thin, opaque, upper side pale yellowish brown, whorls with a wide (covering close to half the width of the whorl or more), vaguely outlined, darker brown band above the suture.

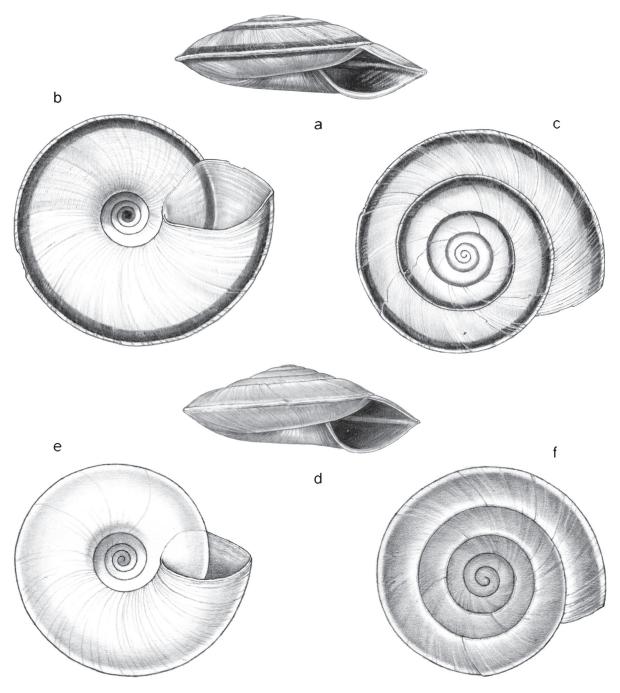


Fig. 162, a-c. *Videna metcalfei* (L Pfeiffer, 1845), a. Frontal view, shell 5.5 mm high, b. Umbilical view, c. Apical view; d-f. *Videna repanda* (Von Möllendorff, 1890), d. Frontal view, shell 3.9 mm high, e. Umbilical view, f. Apical view.

Shell silky above, approx. glossy below. Spire low-conical with straight to convex sides, only slightly raised in some shells. Whorls: First whorls moderately convex, last whorl moderately convex to almost flat, not or hardly compressed towards the periphery. Sculpture. Protoconch with minute, inconspicuous radial wrinkles towards the suture. Teleoconch above the periphery with a microscopical granulation (just visible at 40x magnification), with the granules locally aligned as to suggest a slight, oblique spiral striation; next to this with densely placed, unevenly spaced, low, rounded, raised growth lines, locally developing in radial riblets; below the periphery with a less distinct microsculpture only locally present, growth lines present, locally raised. Spiral sculpture absent. Aperture obtusely quadrangular. Peristome thickened in fully adult shells, and with a slight lip on the basal side. Umbilicus open, wide. Dimensions. Height up to 6.0 mm; width up to 16 mm; ratio height/width 0.33–0.41; fourth whorl 7.0–8.5 mm diam.; last whorl 33–40 % of the shell width; umbilicus up to 4.0 mm wide, which is 21–31 % of the

shell width; number of whorls up to 5 1/2, height aperture up to 3.6 mm; width aperture up to 7.0 mm.

Distribution in Sabah. Scattered localities in N: Balambangan and Banggi islands, Kota Marudu. Elevation range: 0–400 m. In (stunted) coastal forest on limestone bedrock. Distribution elsewhere: Philippines.

Group 2

Videna bicolor (E Von Martens, 1864)

(fig. 163a-c, 164b, map 36e)

Solem 1964: 26; Vermeulen & Whitten 1998: 121, 156; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Tan et al. 2012: 109; Foon et al. 2018: 96; Marzuki et al. 2021: 92. – *Trochomorpha bicolor* Von Martens 1864b: 267; Von Martens 1867: 252; Issel 1874: 404; Tenison Woods 1888: 1029; Aldrich 1889: 25; Godwin-Austen 1891: 42; Pilsbry 1893 (1893–1895): 5; Schepman 1896: 155; Smith 1898a: 29; Von Martens 1908: 261; Van Benthem Jutting 1952: 413; 1959: 141; Saul 1967: 110. – *Helix bicolor* (Von Martens) Pfeiffer 1868: 182. – *Trochomorpha (Videna) bicolor* (E Von Martens) Pfeiffer & Clessin 1881: 83; Wiegmann 1898: 419. – *Helix (Videna) bicolor* (E Von Martens) Tryon 1887: 82. – Type from Indonesia, Sumatra.

(?) *Trochomorpha crassicarinata* auct. Saul, 1967: 110. [Not *Trochomorpha crassicarinata* Fulton].

Description. Shell medium-sized, rather thin, opaque, upper side pale to dark orange-brown to red-brown, whorls with a (narrow) seam of white to pale yellow bordering the upper and lower sutures; in some shells the upper seam reaching down to over half-way the width of the whorl; lower side approx. as the upper, umbilical region white to pale yellow. Shell glossy. Spire (rather) low-conical with straight to convex sides, last whorl sometimes protruding in low-conical shells. Whorls: First whorls moderately convex, last whorl almost flat to slightly convex, somewhat compressed towards the periphery, sometimes somewhat shouldered in shells with a protruding last whorl. Sculpture. Protoconch with minute, inconspicuous radial wrinkles. Teleoconch above the periphery with predominant radial sculpture: Distinct, densely placed, low, rounded radial riblets; below the periphery with growth lines, or inconspicuous radial ribs only. Spiral sculpture above the periphery: First whorls with densely placed, shallow grooves, last whorl with coarser spiral grooves cutting into or through the radial riblets, rather densely placed and deepest towards the suture and the periphery, widely spaced and shallower, or sometimes absent in between; below the periphery spiral grooves moderately spaced at the base and towards the periphery, more widely spaced in between, umbilical area without spiral sculpture. Aperture obtusely quadrangular. Peristome slightly thickened in fully adult shells, with a slight lip on the basal side. Umbilicus open, wide. Dimensions. Height up to 6.5 mm; width up to 16 mm; ratio height/width 0.33-0.52; fourth whorl 6.2-7.8 mm diam.; last whorl 22-35 % of the shell width; umbilicus up to 3.7 mm wide, which is 18-25 % of the shell width; number of whorls up to 6, height aperture up to 3.6 mm; width aperture up to 6.8 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–900 m. In (disturbed) primary forest, stunted coastal woodland and shrubland on limestone bedrock. Sometimes persistent in degraded vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Vietnam (? N part), Malaysia (Peninsula), Singapore, Indonesia (Sumatra, Java, E-wards to Flores, Maluku).

Variability. Generally, the shells are darker brown that other Sabah Videna species, but specimens occur with only a narrow brown band near the periphery. The spire shape is somewhat variable too. Most shells are low-conical with approx. straight sides (as the illustrated), but shells with a higher conical spire, often with convex sides, occur

Note. Extensive anatomical description in Wiegmann (1898).

Videna froggatti (Iredale, 1941)

(fig. 163d-f, map 36f)

Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762. – *Necvidena froggatti* Iredale 1941: 73. – *Trochomorpha froggatti* (Iredale) Van Benthem Jutting 1964: 17; Saul 1967: 110 (*'frogatti'*). – *Helix planorbis* Lesson 1831: 312. – *Helix (Videna) planorbis* (Lesson) Pfeiffer 1855b: 132; Bock 1881: 633; Tryon 1887: 82. – *Trochomorpha planorbis* (Lesson) Wallace 1865: 408; Von Martens 1867: 249; Issel 1874: 403; Tenison Woods 1888: 1029; Aldrich 1889: 25; Godwin-Austen 1891: 41; Pilsbry 1893 (1893–1895): 5; Kobelt 1897: 55; Wiegmann 1898: 427; Von Martens 1908: 261; Van Benthem Jutting 1952: 411; 1959: 142; Maassen 1997: 73. – *Trochomorpha (Videna) planorbis* (Lesson) Pfeiffer & Clessin 1881: 84. – *Videna planorbis* (Lesson) Solem 1964: 25; Maassen 2001: 116. – Type from 'New Guinea'.

[Not Helix planorbis Linne].

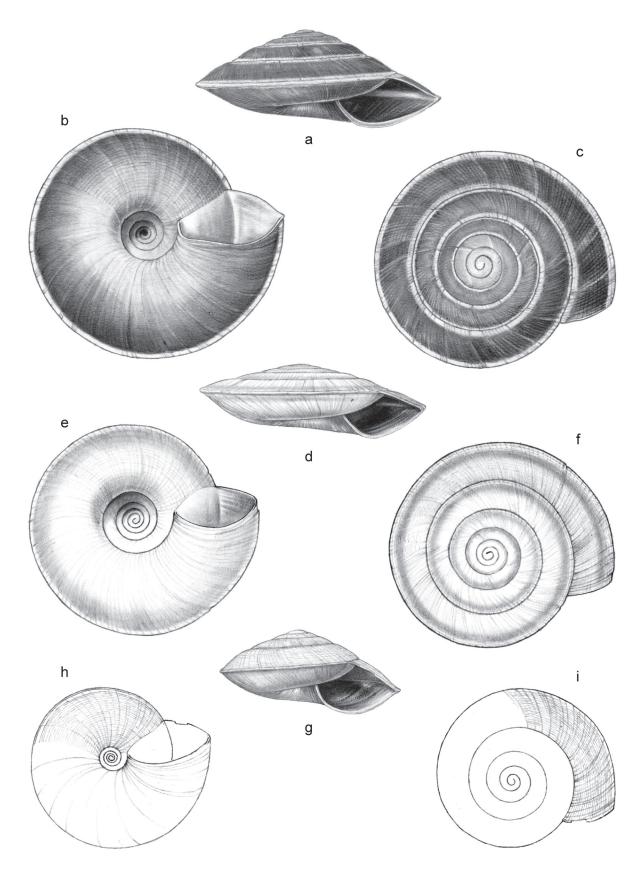


Fig. 163, a–c. *Videna bicolor* (E Von Martens, 1864), a. Frontal view, shell 4.2 mm high, b. Umbilical view, c. Apical view; d–f. *Videna froggatti* (Iredale, 1941), d. Frontal view, shell 4.4 mm high, e. Umbilical view, f. Apical view; g–i. *Videna nepiadel-phos* Vermeulen & Liew, new species, g. Frontal view, shell 3.8 mm high, h. Umbilical view, i. Apical view.

Cross diagnosis. Resembles *Videna bicolor*, differs by the virtual absence of spiral striation on the last whorl (in shells with more than 5 whorls), except for sometimes a few grooves close to the periphery. Generally, the spire is less distinctly raised, the umbilicus is wider (22–31 % of the shell width, versus 18–25 %), and the colored spiral band on the upper surface is less clearly defined, narrower and paler.

Description. Shell medium-sized, rather thin, opaque, pale yellowish (brown), whorls on the upper side usually with a wide (up to approx. half the width of the whorl or more), but vaguely outlined, orange-brown band just above the periphery, which in some shells is only slightly darker that the rest of the shell and hardly discernible, on the lower side slightly darker towards the periphery. Shell shiny. Spire approx. flat with a slightly raised apex to low-conical with straight or slightly convex sides, last whorl sometimes slightly descending. Whorls: First whorls moderately convex, last whorl almost flat to slightly convex, somewhat compressed towards the periphery. Sculpture. Protoconch approx. smooth. Teleoconch above the periphery with predominant radial sculpture: Distinct, densely placed, low, rounded radial riblets; below the periphery with growth lines, or inconspicuous radial ribs only. Spiral sculpture above the periphery: First whorls with (rather) densely placed, shallow grooves, which are more widely and unevenly spaced on the middle whorls, last whorl without spiral grooves, or with 1-3 coarser spiral grooves cutting into or through the radial riblets, towards the periphery, and sometimes a few scattered traces of spiral striation above these; below the periphery moderately spaced spiral striation, often partly absent, sometimes entirely absent; umbilical area without spiral sculpture. Aperture approx. quadrangular. Peristome not or slightly thickened. Umbilicus open, very wide. Dimensions. Height up to 6.8 mm; width up to 18.5 mm; ratio height/width 0.29-0.40; fourth whorl 6.0-9.7 mm diam.; last whorl 29-38 % of the shell width; umbilicus up to 4.8 mm wide, which is 22-31 % of the shell width; number of whorls up to 6, height aperture up to 4.4 mm; width aperture up to 7.5 mm.

Distribution in Sabah. Widespread and common in E; rare elsewhere: Balambangan island, Meliau range, Batu Timbang. Elevation range: 0–800 m. In (disturbed) primary forest and shrubland on limestone bedrock. Sometimes persistent in degraded vegetation. Also in Sarawak, Kalimantan. Distribution elsewhere: Malaysia (Peninsula), Indonesia (Sumatra, Java to West Papua), Philippines, Papua New Guinea.

Note. Extensive anatomical description in Wiegmann (1898).

Videna nepiadelphos Vermeulen & Liew, new species

(fig. 163g-i, map 36d)

Type specimens from Malaysia, Sabah, Tawau Prov., Danum valley Conservation Area (holotype BOR/MOL 14235); Malaysia, Sarawak, Bau area, mount Pangga 3 km ENE of Bau, S slope of hill (paratypes JV 2168/5 shells).

(?) *Trochomorpha* c.f. *timorensis* auct. Butot 1955: 119. – Material from Indonesia, Java, Panaitan island. *Videna timorensis* auct. Schilthuizen & Vermeulen 2003a: 96; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Marzuki et al. 2021: 92.

[Not Trochomorpha timorensis E Von Martens].

Cross diagnosis. Adults differ from Videna bicolor and V. froggatti by the more distinct spiral sculpture which continues down to the aperture, particularly on the upper surface. Adult V. nepiadelphos resemble juveniles of V. bicolor and V. froggatti; the three have comparable coiling densities. Videna nepiadelphos differs by the evenly rounded outer whorl from suture to periphery, with the periphery hardly protruding. The radial sculpture is, as said, also more distinct.

Description. Shell small to medium-sized, rather thin, opaque or slightly translucent, upper side pale yellowish green to pale yellowish brown, whorls often slightly darker towards the periphery, lower side sometimes white. Shell shiny. Spire low-conical with slightly convex sides and a broadly rounded apex. Whorls all moderately convex and evenly rounded towards the periphery, the last whorl sometimes slightly less convex than the first whorls, periphery not or hardly protruding. Sculpture. Protoconch with minute, evenly spaced radial folds towards the suture, as well as a very fine, dense spiral striation. Teleoconch above the periphery with subordinate radial sculpture: Growth lines, locally raised, only on the outer whorl sometimes locally developing in inconspicuous, low, somewhat spaced riblets; below the periphery with growth lines, locally raised, particularly towards the umbilicus. Spiral sculpture above the periphery: Conspicuous, rather densely placed and approx. evenly spaced, fine, narrow and rather deep grooves; below the periphery similar but less conspicuous grooves, disappearing towards the umbilical area which is without spiral sculpture. Aperture somewhat obtusely quadrangular. Peristome not thickened. Umbilicus open, very wide. Dimensions. Height up to 4.8 mm; width up to 9.5 mm; ratio height/width 0.43–0.64; fourth whorl 5.5–7.7 mm diam.; last whorl 37–45 % of the shell width; umbilicus up to 1.9 mm wide, which is 15–27 % of the shell width; number of whorls up to 5 1/4, height aperture up to 3 mm; width aperture up to 4.2 mm.

Distribution in Sabah. Widespread and rather common, but not in N. Elevation range: 0–1100 m. In (disturbed) primary forest and shrubland on limestone bedrock. Sometimes persistent in degraded vegetation. Also in





Fig. 164, a. Videna metcalfei (L Pfeiffer, 1845); b. Videna bicolor (E Von Martens, 1864).

Sarawak, Kalimantan. Distribution elsewhere: Indonesia (Panaitan island off W Java; see note).

Note. Trochomorpha c.f. *timorensis* auct. Butot 1954b: 119, from Indonesia, Panaitan island off Java's W end, seems identical and is provisionally included.

Name derivation. From vήπιος (Ancient Greek) = child, and ἀδελφός = brother.

Family **VERTIGINIDAE** Fitzinger, 1833

Diagnosis for the Sabah species. Snails. Shell with up to 3 1/8–5 1/4 slowly expanding whorls. Shell dextral, minute or very small, as wide as high or higher than wide; spire conical with convex sides to (narrowly) ovoid to cylindrical-ellipsoid; last whorl rounded to obtusely angular at the periphery, last part detached or not. Teleoconch sculpture: Radial sculpture consisting of growth lines locally raised to uneven riblets, sometimes with a periostracal crest, spiral sculpture absent or present, fine; if no spiral sculpture a foveolate microsculpture present in some genera. Aperture with or without teeth. Peristome on the palatal side not thickened, spreading or not. Umbilicus closed or open, narrow or wide. Dimensions: Adults up to 1.4–2.6 mm high, 1.2–2.9 mm wide.

Notes. 1. Unidentified records in literature:

Acinolaemus sp. Schilthuizen et al. 2011: 5.

Systenostoma sp. BO-01 Schilthuizen et al. 2011: 5.

Both are recorded from Balambangan island. We have not seen material, and assume the records are based on mistakes.

2. We apply the family name in a wide sense. MolluscaBase (accessed 1/2021) divides the family: *Boysidia* and *Gastrocopta*: Gastrocoptidae; *Nesopupa*: Vertiginidae s.s.; *Pupisoma* and *Ptychopatula*: Valloniidae.

KEY TO THE GENERA (SABAH SPECIES ONLY)

- 1 Aperture with teeth
 - 2 Spire conical with straight sides. Last part of the last whorl usually detached

Genus Boysidia

- 2 Spire ellipsoid-cylindrical to ovoid to conical with (distinctly) convex sides. Last part of the last whorl attached to the previous whorl
 - 3 Aperture with 1–2 teeth

Genus Pupisoma

- 3 -Aperture with 5 8(-9) teeth
 - 4 Angularis and a parietalis partly fused, or entirely fused to a single lamella with a notched crest

Genus Gastrocopta

4 – Angularis and parietalis well separated

Genus Nesopupa

- 1 Aperture without teeth
 - 5 Teleoconch surface in between radial sculpture foveolate (visible at 40x magnification); spiral sculpture absent

 Genus *Pupisoma*
 - 5 Teleoconch surface in between radial sculpture not foveolate; spiral sculpture present, conspicuous

Genus Ptychopatula

Genus Boysidia Ancey, 1881

Diagnosis for the Sabah species. Spire conical with straight sides. Last part of the last whorl usually detached. Teleoconch surface in between radial sculpture minutely foveolate; spiral sculpture absent. Aperture with 5–7 teeth; a shallow (knob-shaped) angularis and a deep parietalis fused to a single, deeply notched lamella. Peristome spreading.

Boysidia melichroma Vermeulen & Liew, new species

(fig. 165a-c, map 37a)

Type specimens from Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (holotype BOR/MOL 14835; paratypes JV 1865/7 shells).

Cross diagnosis. Identified within the genus by the rudimentary angularis. From *Boysidia salpinx* it also differs by the slenderer spire (excluding the aperture).

Description. Shell very small, thin, approx. opaque, orange-brown. Surface slightly shiny. Spire conical with straight sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl obtusely angular at the periphery, with a slight furrow above and below in the last 1/2 whorl, surface above and below the periphery otherwise approx. flat, basal surface gradually rounded towards the umbilicus, slightly more narrowly rounded towards the aperture. Suture deeply impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with unevenly spaced, flat growth lines of which some are marked as slightly paler lines, in between locally with inconspicuous, low, obtuse, unevenly spaced riblets. Spiral striation absent. Aperture free, with the parietal edge distant from the previous whorl, not or hardly tilted upwards relative to the coiling axis of the spire, approx. circular, gradually expanded towards the aperture; teeth 5–7: A shallow angularis reduced to a slight swelling with an obtuse to acute crest only, fused to a deep short, high parietalis; 1 palatal, 1 basal and 1 columellar lamella, each distinct, high and short, often with a small, low infra-parietalis deep inside the aperture and/or a similar infra-basalis. Peristome gradually spreading, thin. Dimensions. Height of spire excluding free portion of the last whorl 2.3–2.6 mm; width 1.7–1.8 mm; ratio height/width 1.33–1.53; width including free portion of the last whorl 2.6–2.9 mm; umbilicus open, 0.1–0.2 mm wide; number of whorls 3 1/2–3 3/4; height aperture c. 1.3 mm; width 1.2–1.3 mm.

Distribution in Sabah. Baturong-Madai only. Elevation range: 100–200 m. In (disturbed) primary forest on limestone bedrock. Endemic to Sabah.

Similar species elsewhere. The generic placement assumes that the swelling in front of the parietalis is a rudimentary angularis. The fact that the swelling has a somewhat protruding apex in some specimens lends weight to the assumption. The other option, that no angularis is present, would lead to placement in the genus *Anauchen*. Within this genus, *A. khaochongpran* Panha & J B Burch, 2002 and *A. sichang* Panha & J B Burch, 2002 (both from Thailand) have a similar swelling in the upper corner of the aperture. Both differ by having a spire with distinctly concave sides.

Name derivation. From μέλι (Ancient Greek) = honey, and χρῶμα = color.

Boysidia salpinx F G Thompson & Dance, 1983

(fig. 165d–g, map 37a)

Clements et al. 2008: 2762; Marzuki et al. 2021: 103. – *Boysidia (Dasypupa) salpinx* Thompson & Dance 1983: 106. – Type from Malaysia, Sarawak, mount Subis.

Description. Shell very small, thin, opaque, dark red-brown. Surface dull. Spire conical with straight sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl obtusely angular at the periphery, with a slight furrow above and below, particularly towards the aperture, otherwise surface above and below the periphery approx. flat, basal surface rather close to the umbilicus narrowly rounded, developing into an obtuse ridge on the last half-whorl. Suture deeply impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with unevenly spaced, flat growth lines which are marked as greyish lines, in between locally with inconspicuous, low, obtuse, unevenly spaced riblets. Spiral striation absent. Aperture usually free, with the parietal edge slightly distant from the previous whorl, sometimes with the peristome just attached to the previous whorl over a short distance only, slightly to moderately tilted upwards relative to the coiling axis of the spire, approx. circular, spire gradually expanded towards the aperture; teeth 5-7: A shallow angularis and a deep parietalis fused to a single, notched lamella with the front part lower than the back part; 1 palatal, 1 basal and 1 columellar lamella, each distinct, high and short, often with a small, low tubercle-shaped infra-parietalis deep inside the aperture and/or a small, knob-shaped infra-basalis. Peristome gradually spreading, thin. Dimensions. Height of spire excluding free portion of the last whorl 2.0-2.5 mm; width 1.8-2.2 mm; ratio height/width 1.05–1.19; width including free portion of the last whorl 2.6–3.5 mm; umbilicus open, 0.15–0.20 mm wide; number of whorls 3 3/8–3 7/8; height aperture 1.3–1.8 mm; width 1.3–1.7 mm.

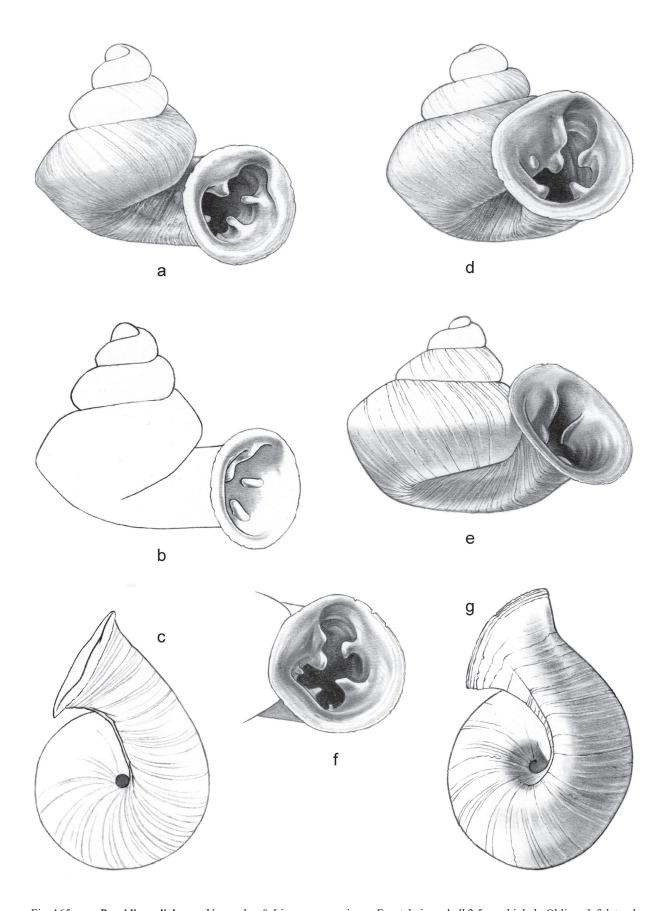


Fig. 165, a–c. *Boysidia melichroma* Vermeulen & Liew, new species, a. Frontal view, shell 2.5 mm high, b. Oblique left lateral view, c. Umbilical view; d–g. *Boysidia salpinx* F G Thompson & Dance, 1983, d. Frontal view, shell 2.1 mm high, e. Oblique left lateral view, shell 2.3 mm high, f. Aperture, frontal view, g. Umbilical view.

Distribution in Sabah. Sapulut only. Elevation range: 400–600 m. In (disturbed) primary forest on limestone bedrock. Also in Sarawak. Endemic to Borneo.

Genus Gastrocopta Wollaston, 1878

Diagnosis for the Sabah species. Spire (narrowly) ovoid to conical with (distinctly) convex sides. Last part of the last whorl attached to the previous whorl. Teleoconch surface in between radial sculpture microscopically foveolate (finer than in *Nesopupa*, barely visible at 40x magnification); spiral sculpture absent. Aperture with 5–7(–9) teeth; among these a shallow angularis and a deep parietalis partly or entirely fused to a single lamella with a notched crest. Peristome on the palatal and basal side spreading.

Gastrocopta avanica (Benson, 1863)

(fig. 166a–c, map 37a)

Pilsbry 1917 (1916–1918): 138; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Phung et al. 2017: 94. – *Pupa avanica* Benson 1863: 428. – *Pupa (Pupilla) avanica* (Benson) Pfeiffer & Clessin 1881: 355. – *Bifidaria avanica* (Benson) Gude 1914: 292. – Type from Myanmar, 'Ava'.

Leucochilus euryomphalum Von Möllendorff 1898: 153; Pilsbry 1917 (1916–1918): 141. – Gastrocopta euryomphala Pilsbry 1934 (1927–1935): 120; Van Benthem Jutting 1952: 356; 1959: 125; Maassen 2001: 73. – Type from Philippines, Busuanga.

Cross diagnosis. Identified among Sabah Gastrocopta by its wide-open umbilicus and its obtusely angular penultimate whorl.

Description. Shell very small, thin, slightly translucent, white. Surface dull or slightly shiny. Spire conical with (distinctly) convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, penultimate whorl obtusely angular at the periphery, last whorl moderately convex, distinctly shouldered towards the aperture, and approx. flat below the shoulder. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch microscopically foveolate (just visible at 40x magnification), locally with unevenly spaced, low, wide, rounded radial riblets. Spiral striation absent. Aperture approx. inverted ovate; teeth 5–6(–9): 1 rather high angularis with its oblique frontal end close to or connecting with the peristome, obliquely next to and connected to it 1 usually more prominent, curved parietalis slightly deeper in the aperture, and sometimes 1 small, knob-shaped tooth on its other side; 1 distinct, approx. horizontal columellaris, usually with 1 smaller, knob-shaped infra-columellaris, 1 large, straight palatalis, and 1–3 approx. knob-shaped supra-palatales, if more than one the upper smallest and closest to, or attached to the peristome. Peristome thin, spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus open, wide. Dimensions. Height 2.0–2.5 mm; width 1.2–1.5 mm; ratio height/width 1.54–1.70; number of whorls 4 1/8–4 5/8; umbilicus 0.2–0.4 mm wide, 14–30 % of the shell width; height aperture 0.7–0.9 mm; width 0.75–0.85 mm.

Distribution in Sabah. Rather common in coastal areas and on islands. Elevation range: 0–100 m; elsewhere up to 1400 m. In woodland, shrubland and plantations. Elsewhere also inland, in seasonally very dry vegetation on limestone bedrock. Distribution elsewhere: Myanmar, Malaysia (Peninsula), Indonesia (Sumatra, islands off the coast of Java), Philippines (Busuanga).

Gastrocopta pediculus (Shuttleworth, 1852)

(fig. 166d-f)

Pilsbry 1917 (1916–1918): 296; Solem 1988: 486; Cowie 1997: 28; Clements et al. 2008: 2762 (see note). – *Pupa pediculus* Shuttleworth 1852: 296. – *Pupa (Vertigo) pediculus* (Shuttleworth) Pfeiffer 1855b: 177. – Type from Marquesas islands.

Cross diagnosis. The configuration of the teeth in the aperture is approx. as in *Gastrocopta avanica*, but the penultimate whorl is not angular, and the umbilicus is closed.

Description. Shell very small, thin, slightly translucent, white. Surface dull or slightly shiny. Spire ovoid, apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, other whorls moderately convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch microscopically foveolate (just visible at 40x magnification), locally with unevenly spaced, low, wide, rounded radial riblets. Spiral striation absent. Aperture approx. inverted ovate; teeth 5–6: 1 rather high angularis with its oblique frontal end close to or connecting with the peristome, obliquely next to and connected to it 1 more prominent, curved parietalis slightly deeper in the aperture; 1 distinct, approx. horizontal columellaris, with or without 1 small, knob-shaped infra-columellaris, 1 rather large, straight palatalis, and 1(–2) lower and shorter supra-palatales. Peristome thin, spreading

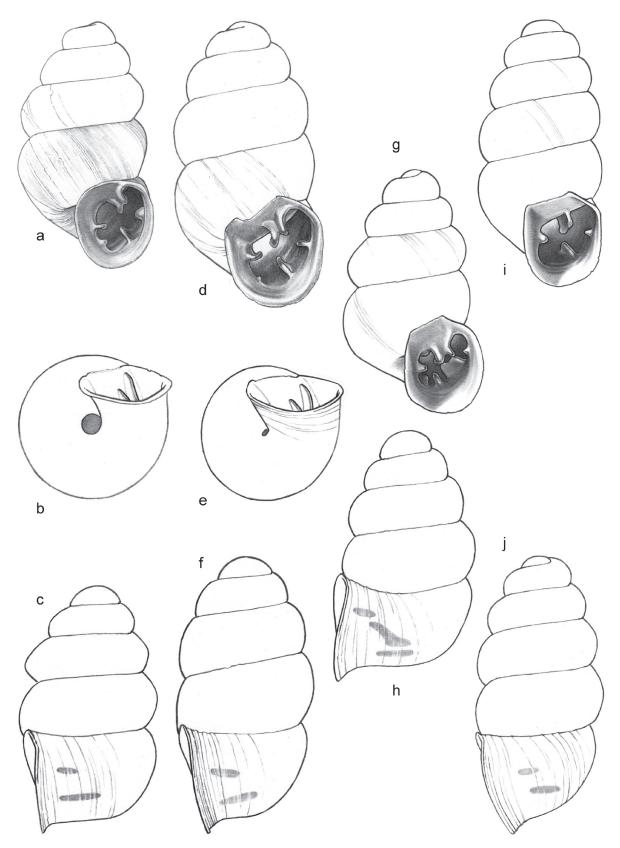


Fig. 166, a–c. *Gastrocopta avanica* (Benson, 1863), a. Frontal view, shell 2.2 mm high, b. Umbilical view, c. Right lateral view with teeth indicated; d–f. *Gastrocopta pediculus* (Shuttleworth, 1852), d. Frontal view, shell 2.5 mm high, e. Umbilical view, f. Right lateral view with teeth indicated, shell 2.4 mm high; g–h. *Gastrocopta recondita* (Tapparone-Canefri, 1883), g. Frontal view, shell 2.3 mm high, h. Right lateral view with teeth indicated, shell 2.2 mm high; i–j. *Gastrocopta servilis* (Gould, 1843), i. Frontal view, shell 2.5 mm high, j. Right lateral view with teeth indicated, shell 2.45 mm high.

on the palatal and basal side, widened and spreading on the columellar side. Umbilicus open, rimate, or closed. Dimensions. Height 2.0–2.6 mm; width c. 1.2 mm; ratio height/width 1.67–2.17; number of whorls 4 1/8–4 1/2; height aperture 0.8–1.0 mm; width 0.7–0.8 mm.

Distribution in Sabah. Not recorded yet. Elsewhere in coastal areas: landward side of mangroves, dunes, coastal shrubland. Elevation range: 0–100 m. Also in Kalimantan. Distribution elsewhere: Vietnam, Philippines, Indonesia (Java and further E) to Australia, E Pacific.

Note. Listed in Clements et al. (2008), but we could not verify this record, and we have not seen any other Sabah material. It can be expected in Sabah in coastal environments because it occurs widespread and has already been found in Kalimantan.

Gastrocopta recondita (Tapparone-Canefri, 1883)

(fig. 166g-h, map 37b)

Pilsbry 1917 (1916–1918): 153; Solem 1988: 496; Vermeulen & Whitten 1998: 79, 144; Clements et al. 2008: 2762; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 95. – *Pupa recondita* Tapparone-Canefri 1883: 106. – *Leucochilus reconditum* (Tapparone-Canefri) Boettger 1891: 270. – Type from Indonesia, Aru islands, Wokam.

Cross diagnosis. Identified among Sabah Gastrocopta by the oblique palatalis.

Description. Shell very small, thin, slightly translucent, white. Surface dull or slightly shiny. Spire ovoid to conical with convex sides; apex rounded. Whorls: Protoconch whorls convex; teleoconch whorls convex, last whorl slightly shouldered towards the aperture, and somewhat rounded below the shoulder. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch microscopically foveolate (just visible at 40x magnification), with growth lines which develop into unevenly spaced, (rather) low, rather narrow, rounded radial riblets. Spiral striation absent. Aperture approx. obtusely (and obliquely) rectangular to inverted ovate; teeth 6–7: 1 prominent angularis with its oblique frontal end close to or connecting with the peristome, obliquely next to and connected to it 1 usually more prominent, curved parietalis slightly deeper in the aperture; 1 distinct columellaris which inwards descends along the columella, 1 distinct, short infra-columellaris, 1 distinct, straight, rather high infra-palatalis of varying length, 1 high, approx. obtusely rectangular, obliquely transverse palatalis with its inward end approaching the infra-palatalis, 1 short supra-palatalis close to, or attached to the peristome. Peristome thin, spreading on the palatal and basal side, somewhat widened and spreading on the columellar side. Umbilicus closed, or open but narrow. Dimensions. Height 1.85–2.30 mm; width 1.15–1.30 mm; ratio height/width 1.58–1.80; number of whorls 4 1/8–5 1/8; umbilicus up to 0.05 mm wide, c. 4 % of the shell width; height aperture 0.80–0.95 mm; width 0.65–0.80 mm.

Distribution in Sabah. Scattered localities in coastal areas and on islands in W; also Sapulut (see note). Elevation range: 0–100 m. In coastal areas, from woodland to denuded cliffs. Elsewhere also inland, in seasonally dry vegetation on limestone bedrock. Distribution elsewhere: From Indonesia (Java, Bali, Tanimbar islands) E-wards to Australia.

Note. The Sapulut record is from forest on limestone deep inland. The species may have been introduced there by agricultural development projects.

Gastrocopta servilis (Gould, 1843)

(fig. 166i–j, map 37c)

Pilsbry 1916 (1916–1918): 70; Solem 1988: 483; Cowie 1997: 28; Vermeulen & Whitten 1998: 79, 144; Schilthuizen et al. 2013: Online supplementary data. – *Pupa servilis* Gould 1843a: 356. – Type from Cuba.

Pupa lyonsiana Ancey 1892: 713. – Gastrocopta lyonsiana (Ancey) Pilsbry 1917 (1916–1918): 141; Van Benthem Jutting 1952: 355. – Type from Hawaii.

Cross diagnosis. Identified among Sabah *Gastrocopta* by the brown-corneous shell, with the angularis and the parietalis placed in line rather than parallel to each other. In some shells the two lamellae are almost entirely fused, in others the back of one is just touching the front of the other.

Description. Shell very small, thin, slightly translucent, brown-corneous. Surface (slightly) shiny. Spire (narrowly) ovoid, apex rounded. Whorls: Protoconch whorls convex; teleoconch whorls convex, last whorl somewhat shouldered towards the aperture, and somewhat rounded below the shoulder. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch microscopically foveolate (just visible at 40x magnification), with growth lines which develop into unevenly spaced, (rather) low, rather narrow, rounded radial riblets. Spiral striation absent. Aperture approx. obtusely (and obliquely) rectangular to inverted ovate; teeth 5–6: 1 prominent angularis with its oblique frontal end close to or connecting with the peristome, at its back connected to 1 parietalis to form a single lamella with a notched crest; 1 distinct, horizontal columellaris, with or without 1 short

infra-columellaris or 1 basalis; 1 distinct, straight, rather high palatalis, 1 short supra-palatalis close to or attached to the peristome. Peristome thin, spreading on the palatal and basal side, (somewhat) widened and spreading on the columellar side. Umbilicus closed. Dimensions. Height 2.15–2.80 mm; width 1.1–1.3 mm; ratio height/width 1.92–2.25; number of whorls 4 5/8–5 1/4; height aperture 0.75–1.10 mm; width 0.70–0.95 mm.

Distribution in Sabah. Recorded from Tun Sakaran Marine Park only, but possibly more widespread. Elevation range: 0–100 m. In coastal areas, from woodland to denuded cliffs. Elsewhere on Borneo also inland, in degraded, seasonally very dry vegetation on limestone bedrock. Introduced. Also in Kalimantan. Distribution elsewhere: Approx. circumtropical. Natural range: Caribbean.

Genus Nesopupa Pilsbry, 1900

Diagnosis for the Sabah species. Spire ellipsoid-cylindrical to ovoid to conical with convex sides. Last part of the last whorl attached to the previous whorl. Teleoconch surface in between radial sculpture distinctly foveolate (clearly visible at 40x magnification); spiral sculpture absent. Aperture with 5–8(–9) teeth; angularis and parietalis well separated. Peristome on the palatal and basal side spreading.

Nesopupa malayana (Issel, 1874)

(fig. 167a, map 37d)

Nesopupa (Insulipupa) malayana Pilsbry 1920 (1918–1920): 342; Thompson & Dance 1983: 105; Maassen 1997: 48; Vermeulen & Whitten 1998: 81, 145; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 97. – Vertigo malayanus Issel 1874: 416. – Pupa malayana (Issel) Pfeiffer 1877: 404; Tenison Woods 1888: 1054; Von Martens 1908: 263. – Pupa (Vertigo) malayana (Issel) Pfeiffer & Clessin 1881: 360. – Type from 'Borneo'.

Description. Shell minute to very small, thin, slightly translucent, (pale) corneous. Surface shiny. Spire approx. cylindrical(-ellipsoid); apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl slightly to moderately convex, somewhat shouldered towards the aperture. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with growth lines which here and there develop into unevenly spaced, low, thin, rounded radial riblets. Spiral striation absent. Aperture approx. ovate; teeth 5–7: 1 low angularis with the oblique frontal end close to or connecting with the peristome, 1 distinct parietalis, rarely with 1 small knob-shaped infra-parietalis, close to the parietalis, 1 rather distinct, approx. horizontal columellaris, rarely with 1 small, knob-shaped infra-columellaris, 1 (rather) small, basalis deep inside, 1 similar palatalis somewhat less deep inside. Peristome thin, spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus closed. Dimensions. Height 1.6–2.3 mm; width 0.90–1.15 mm; ratio height/width 1.73–2.10; number of whorls 4 3/8–5 1/8; height aperture 0.75–0.95 mm; width 0.70–0.80 mm.

Distribution in Sabah. In coastal areas and on islands; scattered localities in W, rare in E (Tun Sakaran Marine Park). Elevation range: 0–100 m, elsewhere up to 400 m. In primary forest, scrubland, degraded vegetation, grassland; elsewhere also inland, in seasonally very dry vegetation on limestone bedrock. Also in Sarawak. Distribution elsewhere: India, Myanmar, Thailand, Vietnam, Cambodia, Malaysia (Peninsula), Indonesia, Philippines, Australia.

Nesopupa moreleti (A D Brown, 1870)

(fig. 167b, map 37e)

Pilsbry 1920 (1918–1920): 339; Van Benthem Jutting 1959: 125; Thompson & Dance 1983: 104; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Foon et al. 2018: 96. – *Pupa moreleti* Brown 1870: 393; Tenison Woods 1888: 1054; Smith 1894b: 458. – *Vertigo moreleti* (A D Brown) Issel 1874: 415. – *Pupa (Vertigo) moreleti* (A D Brown) Pfeiffer & Clessin 1881: 358. – *Staurodon moreleti* (A D Brown) Von Möllendorff 1890: 252. – *Ennea moreleti* (A D Brown) Von Martens 1908: 263. – Type from Malaysia, 'Labuan'.

Cross diagnosis. Differs from *Nesopupa malayana* by the approx. ovoid spire, and the more distinct basalis and palatalis. Also, the shell is usually wider (width 1.15–1.30 mm, versus 0.90–1.15 mm), and the radial sculpture somewhat more conspicuous.

Description. Shell very small, thin, slightly translucent, (pale) corneous to (pale) orange-brown. Surface shiny. Spire ovoid to conical with distinctly convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl moderately convex, somewhat shouldered towards the aperture. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with growth lines which locally develop into unevenly spaced, low, thin, rounded radial riblets; on the first whorls or down to the last whorl often also with widely and approx. evenly spaced radial riblets as above, but higher and more distinct,

sometimes highest around the periphery. Spiral striation absent but granulose sculpture sometimes approx. aligned to spiral lines on the first whorl. Aperture approx. ovate; teeth 5–8(–9): 1 low angularis with the oblique frontal end close to or connecting with the peristome, 1 distinct, curved parietalis, with or without 1 small knob-shaped infra-parietalis, close to the parietalis, 1 distinct, approx. horizontal columellaris, with or without 1(–2) small, knob-shaped infra-columellares, sometimes with 1 small, lamella-shaped infra-basalis deep inside, 1 large, often somewhat curved, rounded basalis deep inside, 1 similar palatalis somewhat less deep inside, and with or without 1 small, knob-shaped supra-palatalis close to or on the peristome. Peristome thin, spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus closed, or open, slit-like. Dimensions. Height 1.9–2.3 mm; width 1.15–1.30 mm; ratio height/width 1.54–1.92; number of whorls 3 7/8–4 5/8; height aperture 0.80–0.95 mm; width 0.75–0.85 mm.

Distribution in Sabah. In coastal areas and on islands; common in W, rare in E (lower Kinabatangan, Tun Sakaran Marine Park). Elevation range: 0–300 m. In primary forest, shrubland, secondary forest. Also in Sarawak. Distribution elsewhere: Indonesia (Sumatra, Natuna islands, E-wards to Tanimbar islands, Misool), Philippines.

Genus Ptychopatula Pilsbry, 1889

Diagnosis for the Sabah species. Spire ovoid to conical with (distinctly) convex sides. Last part of the last whorl attached to the previous whorl. Teleoconch surface in between radial sculpture not foveolate; spiral sculpture present, conspicuous. Aperture without teeth. Peristome on the palatal and basal side not spreading.

Note. Included in Pupisoma in MolluscaBase (accessed 1/2021); see note under Pupisoma.

Ptychopatula circumlitum (Hedley, 1897)

(fig. 168a–d, map 37f)

Maassen 2000: 140; 2001: 72. – *Pupisoma circumlitum* Hedley 1897: 44; Pilsbry 1920 (1920–1921): 34; Solem 1988: 473; Vermeulen & Whitten 1998: 82, 145. – Type from Australia, Queensland.

Cross diagnosis. Differs from *Ptychopatula dioscoricola* by its open umbilicus. Also, the spire is wider on average (width of the third whorl 1.70–1.95 mm, versus 1.4–1.8 mm) and the outline of the spire more conical.

Description. Shell minute, thin, slightly translucent, yellowish brown. Surface shiny. Spire conical with convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl (moderately) convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with growth lines which develop into unevenly spaced, locally densely crowded, low, thin, rounded radial riblets. Spiral sculpture subordinate to the radial sculpture, numerous very fine, densely placed, shallow grooves cutting into the radial sculpture. Aperture approx. transversely elliptic; teeth absent. Peristome thin, not spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus open, sometimes partly covered by the spreading columellar peristome. Dimensions. Height 1.6–2.0 mm; width 1.7–1.9 mm; ratio height/width 0.89–1.09, all for shells of 3 whorls or more; number of whorls up to 3 3/8; diameters of the first three whorls 0.55–0.70 mm, 1.1–1.3 mm, 1.70–1.95 mm respectively; umbilicus 0.15–0.20 mm diam.; height aperture 0.9–1.0 mm; width 0.80–0.95 mm.

Distribution in Sabah. Rare in S and E: Pun Batu, Sapulut, Baturong-Madai, Ulu Segama. Elevation range: 0–600 m. In primary and secondary forest, plantations; on limestone bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Probably widespread from Indochina to Australia.

Ptychopatula dioscoricola (C B Adams, 1845)

(fig. 168f–k, map 38a)

Marzuki et al. 2021: 96. – *Helix dioscoricola* C B Adams 1845: 16. – *Pupisoma (Ptychopatula) dioscoricola* (C B Adams) Hausdorf 2007: 1484. – Type from Jamaica.

Helix orcula Benson 1850a: 251; Pfeiffer 1853 (1853–1860): 357; Reeve 1853 (1851–1854): Pl. 174, fig. 1176. – Helix (Conulus) orcula (Benson) Pfeiffer 1855b: 123. – Pyramidula (Pupisoma) orcula (Benson) Pilsbry 1894 (1893–1895): 52. – Pupisoma orcula (Benson) Godwin-Austen 1910 (1897–1914): 301; Pilsbry 1920 (1920–1921): 31; Van Benthem Jutting 1952: 363; 1959: 127; Saul 1967: 110; Thompson & Dance 1983: 103; Solem 1988: 472; Cowie 1997: 28; Vermeulen & Whitten 1998: 83, 146. – Ptychopatula orcula (Benson) Maassen 2000: 140; 2001: 72; Schilthuizen et al. 2002: 256; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen et al. 2003b: 41; Clements et al. 2008: 2762; Schilthuizen et al. 2011: 5; Schilthuizen et al. 2013: Online supplementary data; Phung et al. 2017: 97. – Type from India.

Pupisoma 'unidentified' Schilthuizen 2004: 95.

Description. Shell minute, thin, slightly translucent, yellowish brown. Surface shiny. Spire ovoid or conical with distinctly convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl (moderately) convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch

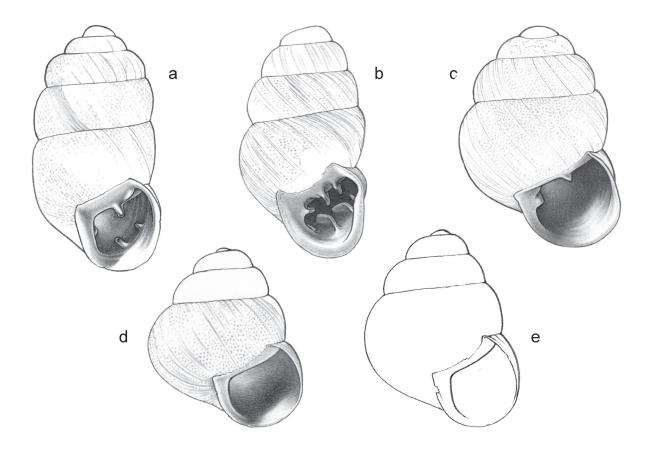


Fig. 167, a. *Nesopupa malayana* (Issel, 1874) frontal view, shell 2.1 mm high; b. *Nesopupa moreleti* (A D Brown, 1870) frontal view, shell 2.0 mm high; c. *Pupisoma lignicola* (Stoliczka, 1871) frontal view, shell 2.0 mm high; d–e. *Pupisoma pul-visculum* (Issel, 1874) frontal views, d. Shell 1.35 mm high, e. Shell 1.5 mm high.

with growth lines which develop into unevenly spaced, locally densely crowded, low, thin, rounded radial riblets. Spiral sculpture subordinate to the radial sculpture, numerous very fine, densely placed, shallow grooves cutting into the radial sculpture. Aperture approx. transversely elliptic; teeth absent. Peristome thin, not spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus closed, a narrow space underneath the slightly lifted columellar peristome. Dimensions. Height 1.6–2.2 mm; width 1.5–2.0 mm; ratio height/width 0.95–1.25, all for shells of 3 whorls or more; number of whorls up to 3 1/2; diameters of the first three whorls 0.50–0.75 mm, 1.0–1.3 mm, 1.4–1.8 mm respectively; height aperture 0.75–1.10 mm; width 0.8–1.3 mm.

Distribution in Sabah. Widespread, common. Elevation range: 0–1100 m. In (disturbed) primary forest, coastal forest and shrubland. Also in secondary woodland. On limestone and sandstone/shale bedrock. Also in Sarawak, Kalimantan. Distribution elsewhere: Africa, Asia, Australia, Pacific.

Notes. 1. Hausdorf (2007) synonymizes *Helix orcula* and *H. dioscoricola* after comparing American and African material. Borneo material strongly resembles American material in shape and size, although the shells are on average slightly higher and narrower (American shells: height 1.3–1.9 mm; width 1.50–1.85 mm; ratio height/width 0.84–1.03; number of whorls up to 3; diameter of the second whorl 1.15–1.30 mm; height and width aperture 0.75–0.90 mm, all according to Hausdorf l.c.). These differences may be because we find up to 1/2 more whorl in our material. As we cannot indicate clear-cut differences between the two, we identify Borneo material as *Ptychopatula dioscoricola*.

2. Hausdorf (2007) mentions the occasional occurrence of 'additional riblets' on the shell in American material, and his fig. 2 illustrates a shell with a sculpture resembling that of *Ptychopatula orcella*. Possibly, the latter is a form of *P. dioscoricola* with distinct sculpture. Investigation is needed.

Ptychopatula orcella (Stoliczka, 1873)

(fig. 168e, map 37f)

Maassen 2000: 140; 2001: 72; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Foon et al. 2018: 96; Marzuki et al. 2021: 99. – *Pupa (pupisoma) orcella* Stoliczka 1873: 33; Pfeiffer & Clessin 1881: 352; Tenison Woods 1888: 1054; Godwin-Austen 1910 (1897–1914): 301. – *Pupisoma orcella* (Stoliczka) De Morgan 1885: 391; Pilsbry 1920 (1920–1921): 29; Vermeulen & Whitten 1998: 82, 146. – *Pyramidula (Pupisoma) orcella* (Stoliczka) Pilsbry 1894 (1893–1895): 52. – Type from Malaysia, Penang.

Cross diagnosis. Differs from *Ptychopatula circumlitum* and *P. dioscoricola* by the prominent, well-spaced radial riblets, next to the fine radial riblets present in all three species of the genus. In general shape, *P. orcella* resembles *P. circumlitum* more than *P. dioscoricola*.

Description. Shell minute, thin, slightly translucent, yellowish brown. Surface shiny. Spire conical with convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl (moderately) convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with growth lines which develop into unevenly spaced, locally densely crowded, low, thin, rounded radial riblets; on the first whorls but sometimes down to the last whorl also with widely and approx. evenly spaced radial riblets as above, but slightly more distinct. Spiral sculpture subordinate to the radial sculpture, numerous very fine, densely placed, shallow grooves cutting into the radial sculpture. Aperture approx. transversely elliptic; teeth absent. Peristome thin, not spreading on the palatal and basal side, widened and spreading on the columellar side. Umbilicus closed, or open, sometimes partly covered by the spreading columellar peristome. Dimensions. Height 1.5–2.0 mm; width 1.45–2.10 mm; ratio height/width 0.89–1.08, all for shells of 3 whorls or more; number of whorls up to 3 3/8; diameters of the first three whorls 0.55–0.70 mm, 1.0–1.3 mm, 1.40–1.90 mm respectively; umbilicus up to 0.2 mm diam.; height aperture 0.8–1.1 mm; width 0.8–1.0 mm.

Distribution in Sabah. Rare in N and W: Banggi island, mount Kinabalu, Keningau. Elevation range: 300–1100 m. In primary and secondary forest, plantations; on limestone and sandstone/shale bedrock. Elsewhere also in coastal areas. Distribution elsewhere: Laos, Thailand, Malaysia (Peninsula), Indonesia (Java, Bali, Tanimbar islands), Philippines.

Note. Possibly a form of Ptychopatula dioscoricola with distinct sculpture; see note under the latter.

Genus Pupisoma Stoliczka, 1873

Diagnosis for the Sabah species. Spire ovoid to conical with (distinctly) convex sides. Last part of the last whorl attached to the previous whorl. Teleoconch surface in between radial sculpture unevenly foveolate (visible at 40x magnification); spiral sculpture absent. Aperture without teeth, or with 1–2 teeth; none in angular position. Peristome on the palatal and basal side slightly spreading or not.

Note. MolluscaBase (accessed 1/2021) includes *Ptychopatula* here. We keep the two genera separate, based on the characters given in the key to the genera.

Pupisoma lignicola (Stoliczka, 1871)

(fig. 167c, map 37f)

Stoliczka 1873: 32; Gude 1914: 34; Pilsbry 1920 (1920–1921): 23; Vermeulen & Raven 1998: 274; Páll-Gergely 2020: 248. – *Pupa lignicola* Stoliczka 1871: 171. – *Pupa (Pupisoma) lignicola* (Stoliczka) Pfeiffer & Clessin 1881: 352. – *Pyramidula (Pupisoma) lignicola* (Stoliczka) Pilsbry 1894 (1893–1895): 52. – Type from Myanmar, 'Moulmein, provincia Tenasserim'.

Pupisoma lignicola (Stoliczka) var. unidentata Godwin-Austen 1910 (1897–1914): 300; Gude 1914: 35. – Type from Myanmar, 'Moulmein'.

Costigo moleculina Van Benthem Jutting 1940: 331; 1952: 353; Thompson & Dance 1983: 104; Maassen 1997: 49. – Pupisoma moleculina (Van Benthem Jutting) Maassen 2000: 142; 2001: 72; Marzuki et al. 2021: 100. – Type from Indonesia, Java.

Cross diagnosis. Distinct among Sabah *Pupisoma* and *Ptychopatula* by the slightly spreading peristome on the palatal and basal side, and usually by the presence of apertural teeth. Juveniles, without a spreading peristome, differ from *Pupisoma pulvisculum* by the narrower, more conical spire.

Description. Shell minute or very small, thin, slightly translucent, pale corneous to (yellowish) brown. Surface shiny. Spire ovoid to conical with distinctly convex sides; apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl (moderately) convex, last whorl moderately convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with growth lines which locally develop into unevenly spaced, low, thin, rounded radial riblets; on the first whorls but sometimes down to the last whorl

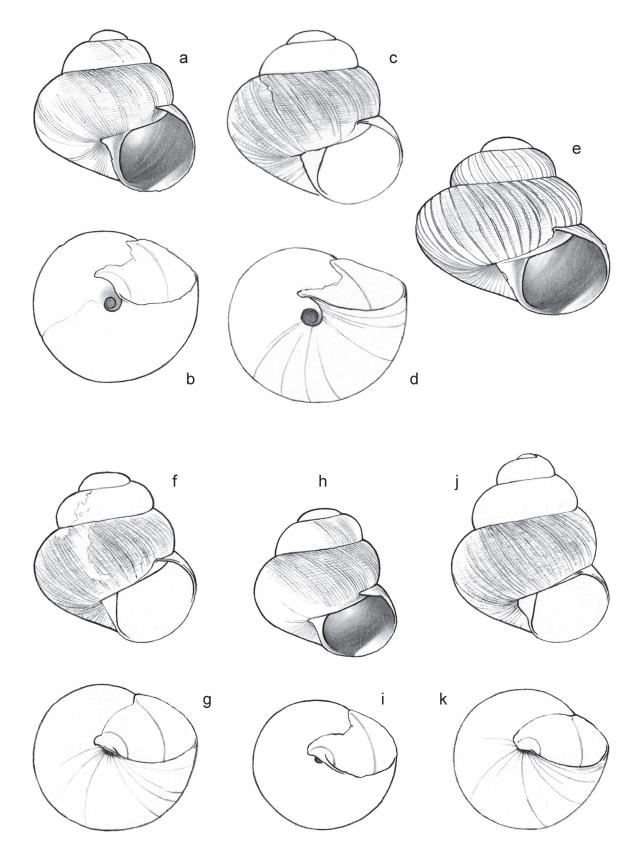


Fig. 168, a–d. *Ptychopatula circumlitum* (Hedley, 1897), a. Frontal view, shell 1.8 mm high, b. Umbilical view, c. Frontal view, shell 1.8 mm high, d. Umbilical view; e. *Ptychopatula orcella* (Stoliczka, 1873) frontal view, shell 2.0 mm high; f–k. *Ptychopatula dioscoricola* (C B Adams, 1845), f. Frontal view, shell 2.0 mm high, g. Umbilical view, h. Frontal view, shell 1.7 mm high, i. Umbilical view, j. Frontal view, shell 2.2 mm high, k. Umbilical view.

also with widely and approx. evenly spaced radial riblets as described above, but slightly more distinct. Spiral striation absent. Aperture obliquely semi-elliptic; teeth absent or 1–2: 1 small, short parietal lamella, 1 small, deep knob-shaped columellaris which is often partly hidden behind the columellar wall. Peristome thin, slightly spreading on the palatal and basal side, distinctly widened and spreading on the columellar side. Umbilicus closed, or open, narrow. Dimensions. Height 1.7–2.3 mm; width 1.05–1.45 mm; ratio height/width 1.31–1.90; number of whorls 3 7/8–4 5/8; diameters of the first three whorls 0.45–0.50 mm, 0.70–0.85 mm, 1.0–1.3 mm respectively; umbilicus up to 0.05 mm wide; height aperture 0.7–1.0 mm; width 0.7–0.9 mm.

Distribution in Sabah. Lower Kinabatangan only. Elevation range: 0–100 m. In primary forest on limestone bedrock. Also in Sarawak. Distribution elsewhere: Myanmar, Laos, Malaysia (Peninsula), Indonesia (Java), Philippines (Palawan, Luzon).

Variability. The apertural teeth are often small, and one or both are absent in some specimens. Maassen (2000) regards *Pupisoma lignicola* and *P. moleculina* as separate species. We cannot distinguish these in the more abundant material available to us.

Notes. 1. Páll-Gergely (2020: 248) gives SEM images of the microsculpture.

2. A single Sabah record in Thompson & Dance (1983). We have not found the species in Sabah.

Pupisoma pulvisculum (Issel, 1874)

(fig. 167d–e, map 38b)

Von Martens 1908: 262; Pilsbry 1920 (1920–1921): 30; Vermeulen & Raven 1898: 275; Schilthuizen & Vermeulen 2003a: 96; Schilthuizen 2004: 95; Clements et al. 2008: 2762; Marzuki et al. 2021: 102. – Helix pulvisculum Issel 1874: 406; Tenison Woods 1888: 1032: Godwin-Austen 1891: 45. – Helix (Monacha) pulvisculum (Issel) Tryon 1887: 191. – Pyramidula (Pupisoma) pulvisculum (Issel) Pilsbry 1894 (1893–1895): 52. – Costigo pulvisculum (Issel) Thompson & Dance 1983: 103. – Type from 'Borneo'.

Description. Shell minute, thin, slightly translucent, (pale) yellowish brown or pale brown. Surface shiny. Spire ovoid, apex rounded. Whorls: Protoconch whorls convex; first teleoconch whorl convex, last whorl (moderately) convex. Suture impressed. Sculpture. Protoconch microscopically foveolate. Teleoconch with a foveolate microsculpture, with scattered growth lines which develop into unevenly spaced, low, thin, rounded radial riblets. Spiral striation absent. Aperture somewhat obliquely semi-elliptic; teeth absent. Peristome thin, not spreading on the palatal and basal side, somewhat widened on the columellar side. Umbilicus approx. closed, or open, narrow. Dimensions. Height 1.4–1.8 mm; width 1.2–1.4 mm; ratio height/width 1.07–1.50; number of whorls 3 1/8–3 7/8; diameters of the first three whorls 0.35–0.50 mm, 0.60–0.95 mm, 0.80–1.25 mm respectively; umbilicus up to 0.05 mm wide; height aperture 0.7–0.8 mm; width 0.55–0.70 mm.

Distribution in Sabah. Widespread, rather common. Elevation range: 0–1200 m. In primary and secondary forest on limestone bedrock. Also in Sarawak, Kalimantan. Endemic to Borneo (?, see note).

Variability. Juveniles have the columellar side of the aperture straight or slightly sinuous, rather than rounded. This character is rarely retained in adult shells.

Note. We have seen similar shells from Indonesia, Sulawesi.

Subclass: HETEROBRANCHIA Order: SYSTELLOMMATOPHORA

Family RATHOUISIIDAE Heude, 1885

Diagnosis for the Sabah species. Slugs without shells. Animal semi-circular to triangular in section, dorsally keeled. No caudal horn. Mantle (notum, see fig. 170a–b) covering the entire dorsal side of the animal except for the tentacles, with the edges fused to the body (edges cannot be lifted), laterally rounded (perinotum); surface papillose. Ventral side divided: A median foot, separated from the ventral edges of the notum (the hyponota) by a groove (the pedal groove); hyponota touching the substrate when creeping. Tentacles 4; upper pair with eyes; lower pair bifid, each with a proximal lobe on the ventral side. Hermaphrodites. Male and female genital pores separated; female pore in the right pedal groove at a distance posterior to the tentacles, together with anus and respiratory pore; male pore behind the right lower tentacle.

Notes. 1. The lobes at the base of the lower pair of tentacles touch the substrate laterally to the mouth when the animal creeps.

2. One of the least studied gastropod families in Asia. Species have been distinguished on some external characters and color patterns. With little material at hand, we can only do the same. Revision of this family is needed.

Genus Atopos Simroth, 1891

Note. Unidentified record in literature:

Atopos sp. 2 Schilthuizen & Liew 2008: 296. Material from mount Kinabalu, at 2600 m alt.; specimen lost.

Atopos punctata Collinge, 1902

(fig. 169a, map 38c)

Collinge 1902: 90; Schilthuizen & Liew 2008: 296. - Type from Malaysia, Pahang.

Description. Animal narrowly elliptic, almost worm-like in outline when creeping; sole approx. 1/3 of the body width or slightly less. Dorsal side with a low, narrow median ridge along its entire length; surface finely papillose with pale ochre-yellow and with brown papillae, the brown papillae predominant along the median line, forming an uneven, sharply delimitated pattern of large, partly interconnected blotches, the pale ochre-yellow papillae predominant along the sides, with brown papillae arranged in thin rows; dorsal side also with widely scattered, slightly larger, black papillae; ventral side ochre yellow. Tentacles ochre-yellow. Female pore situated at approx. 20 % the body length (measured from the head). Dimensions. Body length: 30–35 mm; body width: c. 4 mm.

Distribution in Sabah. Tun Sakaran Marine Park only. Elevation range: 200–300 m. In degraded environments. Distribution elsewhere: Malaysia (Peninsula).

Atopos rapax Vermeulen & Liew, new species

(fig. 169b-d, map 38c)

Type specimen from Malaysia, Sabah, Kinabatangan river valley, Batu Tomanggong Besar (holotype BOR/MOL 3418).

Atopos sp. Schilthuizen et al. 2006: 1856.

Atopos sp. 1 Clements et al. 2008: 2762; Schilthuizen & Liew 2008: 294.

Cross diagnosis. Differs from *Atopos punctata* by the obtusely keeled notum, with a rather coarsely papillose surface and a largely greyish hue, the white proximal and distal end excepted.

Description. Animal narrowly elliptic, almost worm-like in outline when creeping; sole less than 1/4 of the body width (in preserved material). Dorsal side with a low, wide, rounded median ridge along its entire length, which is proximally indistinct and starts a little behind the front edge of the notum; surface rather coarsely papillose, particularly coarse close to the front edge, with white and grey-brown papillae, the grey-brown papillae predominant along the median line, leaving a few pale patches only, the white predominant along the sides, proximal and distal end of the notum white; dorsal side also with scattered, slightly darker grey papillae; ventral side white. Tentacles: Upper grey, lower white. Female pore situated at approx. 20 % the body length (measured from the head; measurement somewhat uncertain due to the state of the material). Dimensions. Largest specimen 22 mm long, c. 3 mm wide.

Distribution in Sabah. Confirmed records from lower Kinabatangan only. Elevation range: 0–100 m. In (disturbed) forest on limestone bedrock. Distribution elsewhere: Unknown.

Similar species elsewhere. Atopos sp. 2 Tan & Chan (2009: fig. 3, 4, 6) and Atopos sp. Tan et al. (2012: 33) resemble A. rapax but has the grey back of the notum separated from the lighter sides by a faint dark line. Further investigation is needed.

Notes. 1. All material available is juvenile.

- 2. Nocturnal. Observed preying on *Plectostoma fraternum*, see fig. 171d. It reaches the soft parts through the aperture or by scraping a hole in the shell wall with its radula; see Schilthuizen et al. (2006), Schilthuizen & Liew (2008).
- 3. Found on a single locality, but *Plectostoma* shells with abraded patches on the shell wall, some with a hole in the center, are found throughout Sabah and elsewhere on Borneo.

Name derivation. From rapax (Latin) = tearing, referring to its carnivorous lifestyle.

Family VERONICELLIDAE Gray, 1840

Diagnosis for the Sabah species. Slugs without shells.

Animal dorsoventrally flattened, dorsally not or hardly keeled. No caudal horn. Mantle (notum, see fig. 170a—b) covering the entire dorsal side of the animal except for the tentacles, with the edges not fused to the body (edges can be lifted), laterally keeled (perinotum); surface finely granulose. Ventral side divided: A narrow median foot, separated from the wide ventral continuations of the notum (the hyponota) by a groove (the pedal groove); hyponota (almost) touching the substrate when creeping. Tentacles 4; upper pair with eyes; lower pair distally bifid. Hermaphrodites. Male and female genital pores separated; female pore in the right hyponotum; male pore in the right pedal groove. Anus and respiratory opening at the posterior end of the foot.

Notes. 1. Occasionally, animals are found with a transversely rugose notum with uneven white and green patches, see fig. 171b. This does not seem to slow the animals down, and Schilthuizen et al. (2008: 292) depict an individual with eggs. They suggest that a fungal or bacterial infection may be the cause. Further investigation is needed.

2. We only give diagnostic character combinations on species level.

Genus Laevicaulis Simroth, 1913

Laevicaulis alte (Férussac, 1821)

(fig. 170a-c, 171a, map 38d)

Rensch 1932: 128; Van Benthem Jutting 1952: 330; 1959: 122; Cowie 1997: 38; Maassen 1997: 47; Vermeulen & Schilthuizen 1998: 56, 140; Maassen 2001: 58; Gomes 2007: 89; Gomes et al. 2008b: 590; Schilthuizen & Liew 2008: 292; Tan et al. 2012: 90. – *Vaginulus alte* Férussac 1821 (1821–1822): Limaces 14. – *Meisenheimeria alte* (Férussac) Grimpe & Hoffmann 1925: 26; Hoffmann 1825: 120, 226. – Type from India, Pondicherry.

Cross diagnosis. Differs from *Semperula wallacei* by the female pore which is situated close to the pedal groove (versus approx. half-way the width of the hyponotum).

Description. Animal elliptic-oblong in outline when creeping; sole approx. as wide as the hyponota or slightly narrower (approx. 1/3 of the body width or slightly less). Dorsal side densely granulose, light yellowish grey to dark grey, with or without darker spots, or almost black, dorsal side usually with a pale-yellow median stripe, ventral side of paler color. Female pore situated slightly beyond half-way the body length (measured from the head), close to the pedal groove. Dimensions. Body length: 50–80 mm; body width: 20–30 mm.

Anatomy. Penis 4.5–8.0 mm long, cylindrical with a collar-like ring near the base, only slightly curved, distally tapering to an obtuse apex, surface smooth, pore apical.

Distribution in Sabah. Kota Kinabalu area only. Elevation range: 0–100 m. Urban areas, on wasteland. Introduced, an agricultural pest elsewhere. Distribution elsewhere: Pantropical. Natural range: Africa.

Genus Semperula Grimpe & Hoffmann, 1924



Fig. 169, a. *Atopos punctata* Collinge, 1902; b-d. *Atopos rapax* Vermeulen & Liew, new species, b-c. Subadults; d. Juvenile predating on *Plectostoma concinnum*.

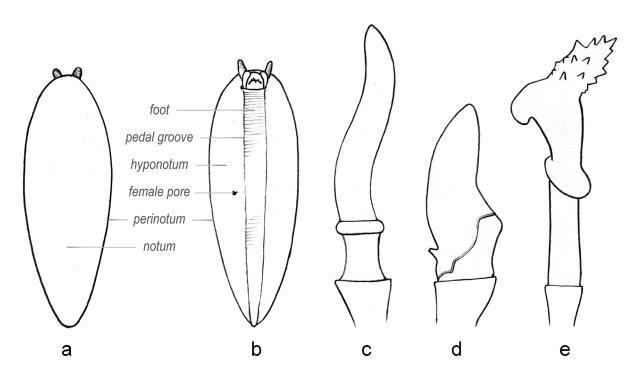


Fig. 170, a–c. *Laevicaulis alte* (Férussac, 1821), a. Animal, dorsal view, b. Animal, central view, c. Penis, 6.1 mm long; d. *Semperula wallacei* (Issel, 1874), penis, 2.9 mm long; e. *Valiguna flava* (Heynemann, 1885), penis, 8.3 mm long.

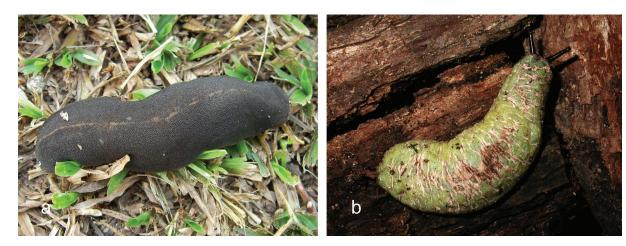


Fig. 171, a. Laevicaulis alte (Férussac, 1821); b. Unidentified veronicellid with the dorsal notum mottled with white and green.

Hoffmann 1941: 233; Van Benthem Jutting 1952: 334; 1959: 124; Maassen 2001: 59; Gomes 2007: 88; Gomes et al. 2008b: 594 Schilthuizen & Liew 2008: 293. – *Vaginula wallacei* Issel 1874: 385; Godwin-Austen 1891: 24; Schepman 1896: 146. – *Veronicella wallacei* (Issel) Von Martens 1908: 263. – Type from Malaysia 'Sarawak'.

Description. Animal elliptic-oblong in outline when creeping; sole distinctly narrower than the hyponota (approx. 1/5 of the body width). Dorsal side sparsely granulose, pale yellow to pale ochre, spotted or marbled with dark grey, with or without a pale median stripe, ventral side pale yellow. Female pore situated slightly beyond half-way the body length (measured from the head), approx. half-way the width of the hyponotum. Dimensions. Body length: 30–45 mm; body width: 10–14 mm.

Anatomy. Penis 2.0–3.0 mm long, (ovoid-)conical without a ring near the base, only slightly curved, obtuse, surface smooth, pore lateral.

Distribution in Sabah. Widespread but few records: Kota Kinabalu area, Sepilok. Possibly under-recorded. Elevation range: 0–100 m. Urban areas, wasteland, and gardens. Also in Sarawak, Kalimantan. Introduced? Distribution elsewhere: SE Asia, Pacific.

Genus Valiguna Grimpe & Hoffmann, 1925

Valiguna flava (Heynemann, 1885)

(fig. 170e, map 38f)

Gomes 2007: 84; Gomes et al. 2008a: 164; 2008b: 595; Schilthuizen & Liew 2008: 292; Marzuki et al. 2021: 105. – *Vaginula flava* Heynemann 1885: 10. – Syntypes from 'Borneo', and Nias island off Sumatra. *Valiguna isseli* Hoffmann 1941: 234 – Type from 'Borneo'.

Cross diagnosis. Differs from *Laevicaulis alte* and *Semperula wallacei* by the female pore in the right hyponotum, which is situated slightly before half-way the body length (measured from the head) (versus slightly beyond half-way the body length).

Description. Animal elliptic in outline when creeping; sole distinctly narrower than the hyponota (approx. 1/5 of the body width). Dorsal side sparsely granulose, pale ochre to dark red-brown, with scattered black spots, usually with a pale median line; ventral side pale brown. Female pore situated slightly before half-way the body length (measured from the head), and slightly closer to the pedal groove than to the outer edge of the hyponotum. Dimensions. Body length: 45–60 mm; body width: 22–30 mm.

Anatomy. Penis 4.0–8.3 mm long, cylindrical with a collar-like ring approx. half-way along its length, with a distinctly hooked, obtuse apex with a conical protuberance at the base of the curvature, which is covered with spines, surface otherwise smooth, pore apical.

Distribution in Sabah. Widespread but rare: Tenom, mount Kinabalu, Danum valley. Possibly under-recorded. Elevation range: 100–500 m. In (disturbed) primary forest on sandstone/shale bedrock. Also in Sarawak. Distribution elsewhere: Indonesia (Sumatra).

Species of uncertain status and excluded species

Species of uncertain status

Note. The species are listed alphabetically under their original name combination.

Amphidromus everetti var. connectens Fulton, 1896

Fulton 1896: 87. – Type from 'N. Borneo'.

Note. Laidlaw & Solem (1961: 585) suggest that it originates from Palawan. It is a taxon of uncertain status. MolluscaBase (accessed 8/2021) lists *A. everetti* Fulton, 1896 as a junior subjective synonym of *A. quadrasi* Hidalgo, 1887.

Cyclostoma tenebricosum A Adams & Reeve, 1850

A Adams & Reeve 1850 (1848–1850): 57. – Leptopoma tenebricosum (A Adams & Reeve) Pfeiffer 1852b: 117; 1858: 76; Vermeulen 1999: 157. – Cyclophorus tenebricosus (A Adams & Reeve) Pfeiffer 1865: 96. – Japonia (Lagochilus) tenebricosa (A Adams & Reeve) Von Martens 1908: 256. – Type from 'Balambangan, Borneo'.

Note. 1. Listed for 'Kinabalu' by Von Martens (1908). Resembles *Leptopoma perlucidum*, and possibly identical with this species. Differs by the wide brown spiral bands such as those occurring in Kalimantan material of *L. perlucidum*. We have not seen Sabah material that can be attributed to *L. tenebricosum*; its status is uncertain, see Vermeulen (1999).

2. The publication date of Cyclostoma tenebricosum is given as 1848 in MolluscaBase (accessed 1/2021).

Helix ceroconus L Pfeiffer, 1864

Pfeiffer 1864 (1863): 523; 1868: 84. – *Trochomorpha ceroconus* (L Pfeiffer) Von Martens 1867: 258; Issel 1874: 405; Tenison Woods 1888: 1027; Godwin-Austen 1891: 42; Von Martens 1908: 262. – Type from Malaysia, 'Labuan island'.

Note. Possibly a Geotrochus, but we cannot place it with any certainty.

Excluded species

Note. 1. The species are listed alphabetically under their original name combination.

2. See also the note on *Helix obliquata* Reeve, 1852, under the description of *Hemiplecta densa*.

Cyclostoma spiracellum A Adams & Reeve, 1850

A Adams & Reeve 1850 (1848–1850): 56. – *Alycaeus (Dicharax) spiracellum* (A Adams & Reeve) Von Martens 1908: 257. – *Dicharax spiracellum* (A Adams & Reeve) Páll-Gergely 2019: 192; Páll-Gergely et al. 2020a: 117. – Type from 'Borneo.'

Note. Recorded for '? Kinabalu' in Von Martens (1908) but the species is native to Korea, see Páll-Gergely (2019). We exclude it from the Borneo fauna.

Helix aglaja Reeve, 1854

Reeve 1854 (1851–1854): Pl. 199, fig. 1396; Pfeiffer 1855 (1854b): 289 ('aglaia'). – Everettia aglaja (Reeve) Godwin-Austen 1891: 35 ('aglaia'). – Type from Malaysia 'Sarawak'.

Note. Recorded from Sabah territory by Godwin-Austen (1891). We have not found the species in Sabah, and we assume that the record is based on misidentification.

Helix antiqua A Adams & Reeve, 1850

A Adams & Reeve 1850 (1848–1850): 61; Pfeiffer 1854 (1853–1860): 400; Reeve 1852 (1851–1854): Pl. 77, fig. 402; Godwin-Austen 1891: 44. – *Papuina antiqua* (A Adams & Reeve) Pilsbry 1891 (1891–1892): 28; 1894

(1893–1895): 141; 1895 (1893–1895): 344; Von Martens 1908: 262; Van Benthem Jutting 1965: 284. – Type from 'Usang, Borneo'.

Note. Originally described as a species from Borneo but according to Pilsbry (1891) a Papuan species; see also Van Benthem Jutting (1965). We exclude it from the Borneo fauna.

Helix borneensis L Pfeiffer, 1850

Pfeiffer 1850 (1849): 127; 1853: 70; Reeve 1854 (1851–1854): Pl. 196, fig. 1379. – *Nanina (Ryssota) borneensis* (L Pfeiffer) Pfeiffer 1855b: 121 ('*Rhyssota*'); Von Martens 1867: 238; Pfeiffer & Clessin 1881: 53; Godwin-Austen 1891: 29. – *Nanina borneensis* (L Pfeiffer) Issel 1874: 35; Tryon 1886: 29; Tenison Woods 1888: 1023. – Type from 'Borneo'.

Note. Probably based on a wrongly labeled shell; it resembles *Ryssota ovum* (Valenciennes, 1827) from the Philippines. We provisionally exclude it from the Bornean fauna.

Helix doriae Dohrn, 1881

Dohrn 1881; 67. – Type from 'the northern part of the island of Borneo'.

Note. See under H. palawanica.

Helix germanus Reeve, 1852

Reeve 1852 (1851–1854): Pl. 74, fig. 385; Pfeiffer 1853: 222; 1854 (1853–1860): 383; 1859: 261; 1868: 338; Issel 1874: 408; Tenison Woods 1888: 1040; Godwin-Austen 1891: 44. – *Helix (Camaena) germanus* Pfeiffer & Clessin 1881: 190. – *Helix orientalis* A Adams & Reeve 1850 (1848–1850): 61. – Type from 'Borneo'. [Not *Helix orientalis* Gray].

Note. Origin given as 'Borneo' by A Adams & Reeve (1848–1850) but as 'Japonia (A Adams)' according to Pfeiffer (1868: 338), with Borneo only mentioned with a question mark. We have not found anything like this species and exclude it from the Sabah fauna.

Helix palawanica L Pfeiffer, 1855

Pfeiffer 1855a: 107; Kobelt 1880 (1880–1897): 577. – *Helix (Camaena) palawanica* (L Pfeiffer) Pfeiffer 1855b: 138; Pfeiffer & Clessin 1881: 190. – Type from 'Palawan Passage, near Borneo'.

Helix monochroa G B Sowerby I 1841: 1; Pfeiffer 1848a: 330; 1850 (1841–1850): 326; Dohrn 1889: 61. – Helix (Camaena) monochroa (G B Sowerby I) Pfeiffer 1855b: 138; Pfeiffer & Clessin 1881: 1890. – Camaena (Phoenicobius) monochroa (G B Sowerby I) Pilsbry 1894 (1893–1895): 104. – Type from Philippines, Tablas. Helix doriae Dohrn 1881: 67. – Type from 'the northern part of the island of Borneo'.

Note. Dohrn (1889) and Pilsbry (1893–1895) list *H. palawanica* and *H doriae* as junior subjective synonyms of *H. monochroa*. Dohrn (1889) questions the origins of both *Helix doriae* (Borneo) and *H. monochroa* (Tablas), and suggests that *H. palawanica* may be a Palawan endemic. We have not found any material like it on Sabah territory and exclude it from the Sabah fauna.

Helix trailli L Pfeiffer, 1855

Pfeiffer 1855a: 107; Kobelt 1880 (1880–1897): 576; Dohrn 1889: 60. – Helix (Camaena) trailli (L Pfeiffer) Pfeiffer 1855b: 138; Pfeiffer & Clessin 1881: 189. – Helix (Hadra) trailli (L Pfeiffer) Smith 1893a: 350. – Camaena (Phoenicobius) trailli (L Pfeiffer) Von Martens 1908: 262 ('Camena'). – Type from 'Palawan Passage, near Borneo'.

Note. Exact provenance uncertain. It could be from Sabah territory, but we have not found anything like it on Banggi and Balambangan islands. Dohrn (1889) lists it from Palawan. We provisionally exclude it from the Sabah fauna.

Leptopoma signatum L Pfeiffer, 1857

Pfeiffer 1857 (1856b): 338; 1858: 71; Reeve 1862a: Pl. 7, fig. 40; Von Martens 1867: 149; Issel 1874: 63; Godwin-Austen 1889: 336; Kobelt & Von Möllendorff 1897c: 79; Kobelt 1902: 14; Von Martens 1908: 278; Ver-

meulen 1999: 152. – Cyclostoma signatum Pfeiffer 1858: 71. – Type from 'Borneo'.

Note. Provenance uncertain. We have not found anything like it on Borneo and provisionally exclude it from the Bornean fauna. The type material differs from *Leptopoma perlucidum* by having a distinctly spreading, convex peristome, which abruptly narrows towards the upper corner, and by having oblique brown markings on the shell.

Rhytida (Macrocycloides) densesculpta B Rensch, 1932

Rensch 1932: 5. – *Macrocycloides densesculpta* (B Rensch) Schilthuizen et al. 2011: 5. – Type from Indonesia, Sumba, Waigapu.

Note. Recorded from beach drift material from Banggi island. The species was mistakenly described as a rhytidid land snail by Rensch (1932) and appeared as such in Sabah literature. It is a junior subjective synonym of *Sigaretornus planus* (A Adams, 1850) (Tornidae), a marine species.

Species listed by Von Martens (1908)

The following species are recorded for 'Labuan-Brunei' in Von Martens (1908). They are native to Borneo, but do not occur in the area covered in this guide.

Alycaeus (Alycaeus) congener (E A Smith): p. 257.

Alycaeus (Alycaeus) galbanus (Godwin-Austen): p. 257.

Cyclophorus (Glossostylus) niahensis (Godwin-Austen): p. 256.

Cyclotus (Opisthoporus) gwendolae (Godwin-Austen): p. 256.

Cyclotus (Opisthoporus) hungerfordi (Godwin-Austen): p. 256.

Diplommatina (Diplommatina) baritensis (E A Smith): p. 258.

Note. Probably based on misidentified material of *D. plecta* and *D. tenuilabiata* (see references with these species).

Diplommatina (Sinica) niahensis (Godwin-Austen): p. 258.

Everettia planior (E A Smith): p. 260.

Gastroptychia moluensis (Godwin-Austen): p. 258.

Gastroptychia sulphurea (Godwin-Austen): p. 258.

Georissa niahensis (Godwin-Austen): p. 259.

Japonia (Lagochilus) barbata (L Pfeiffer): p. 255.

Opisthostoma (Geothauma) grandispinosum (Godwin-Austen): p. 258.

Pterocyclos niahensis (Godwin-Austen): p. 256.

Xesta moluensis (E A Smith): p. 260.

The following species are recorded for 'Kinabalu' in Von Martens (1908). They are native to Borneo, but their known range is widely distant from Sabah. We have never found them in the Kinabalu area, and we assume that these records are based on mistakes.

Diplommatina (Diplommatina) aldrichi Godwin-Austen: p. 258.

Diplommatina (Sinica) onyx (Fulton): p. 258.

Diplommatina (Diplommatina) spinosa (Godwin-Austen): p. 258.

Japonia (Lagochilus) rabongensis (E A Smith): p. 256.

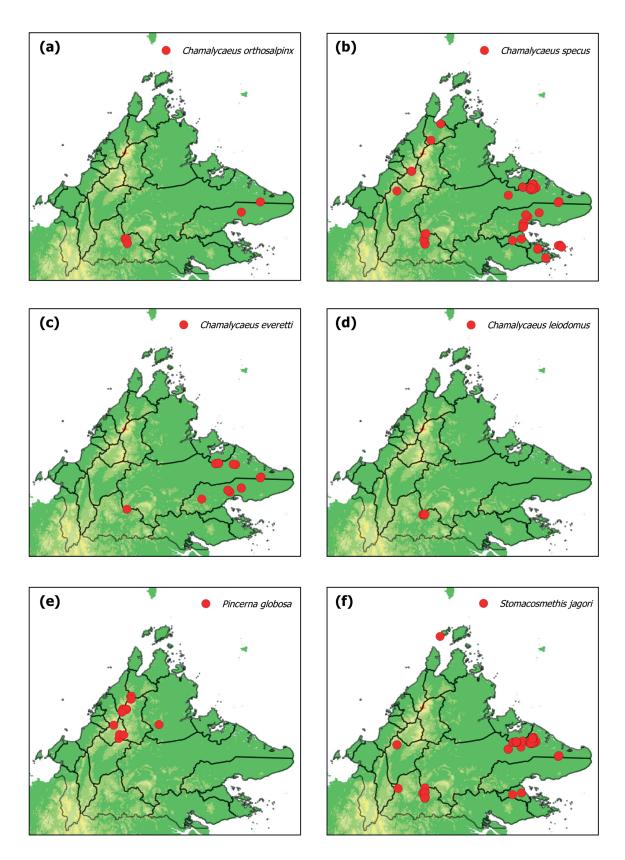
Japonia (Lagochilus) tenebricosa (A Adams & Reeve): 256.

Note. See *Cyclostoma tenebricosum under* 'Species of uncertain position'.

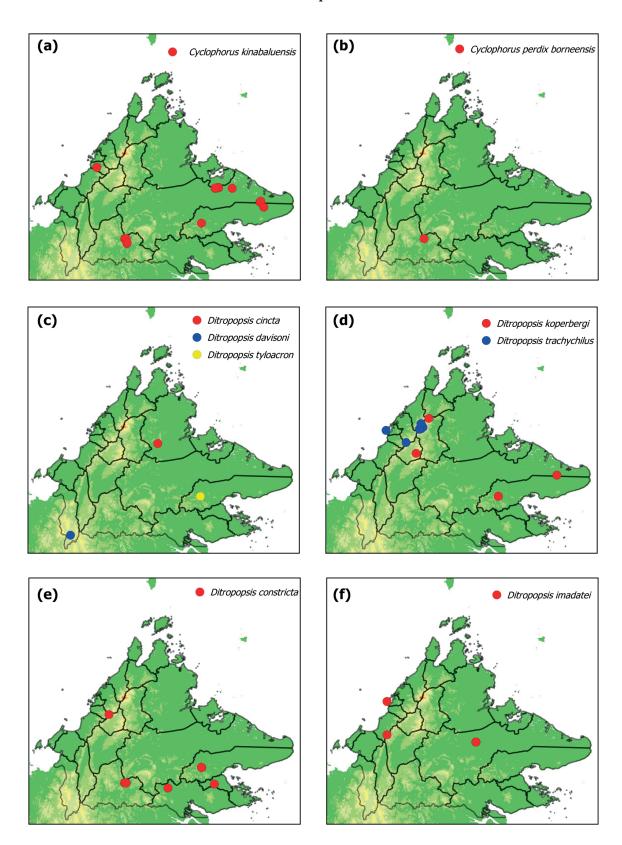
Pupina (Tylotoechus) evansi (Godwin-Austen): p. 257.

Raphaulus kuekenthali (Kobelt): p. 257.

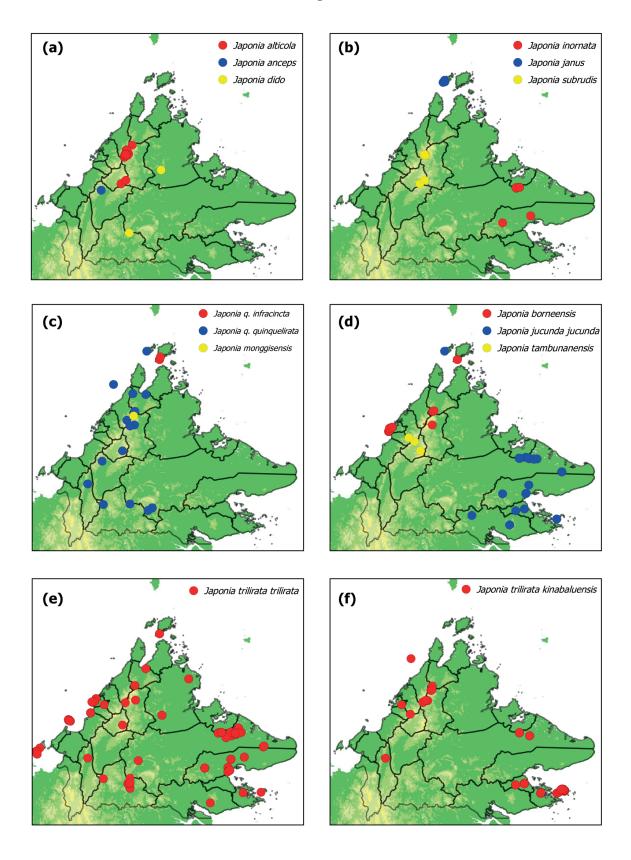
Distribution maps

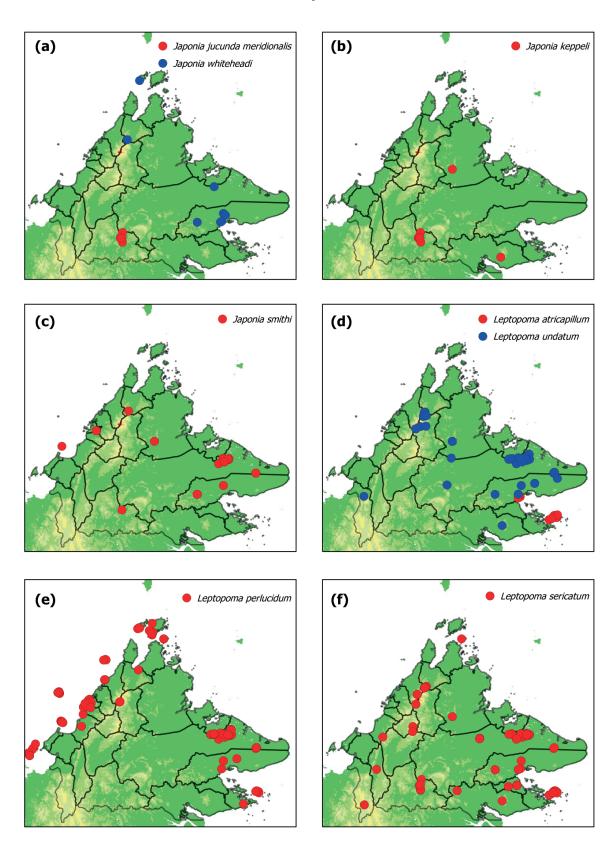


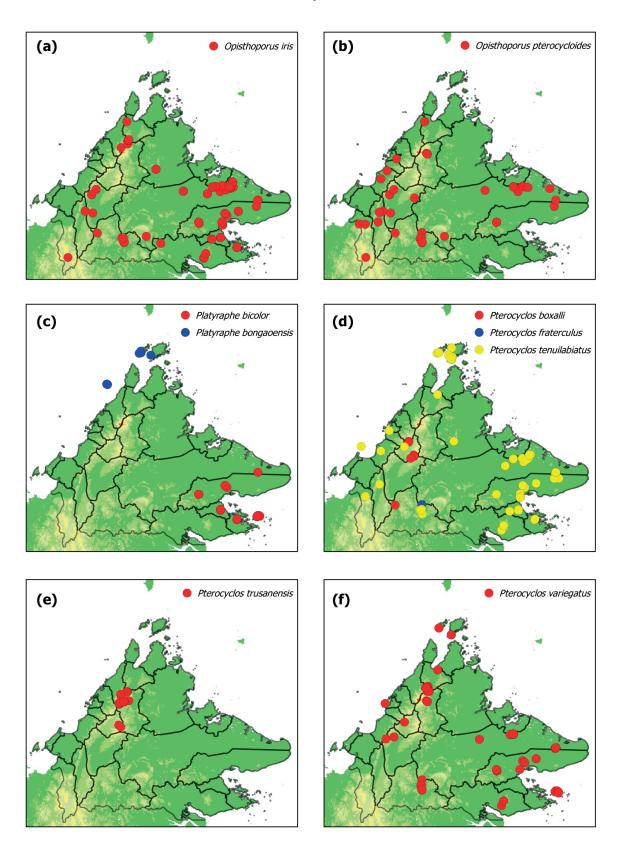
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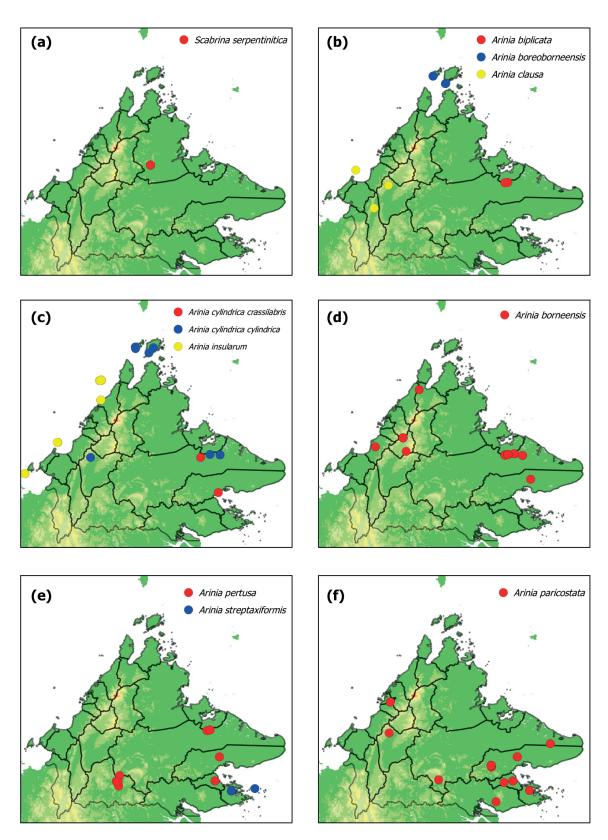


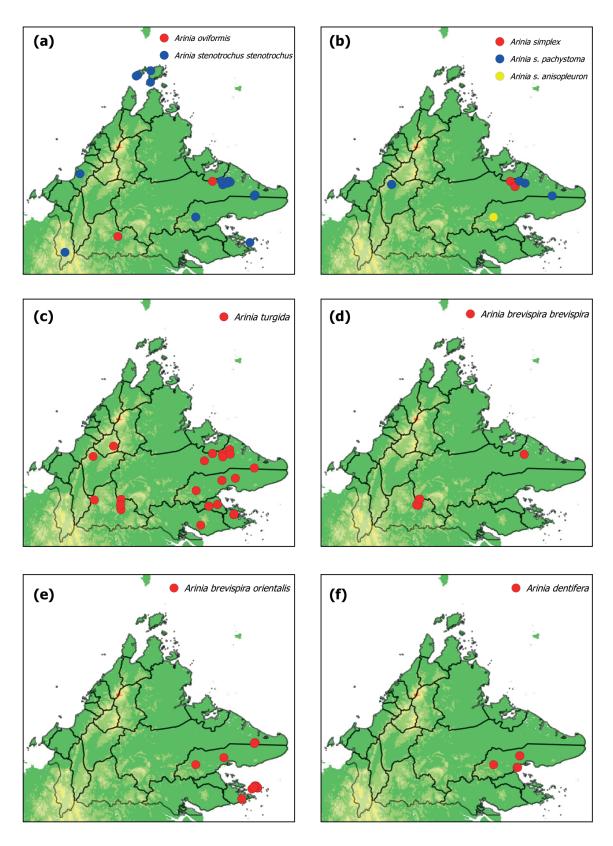
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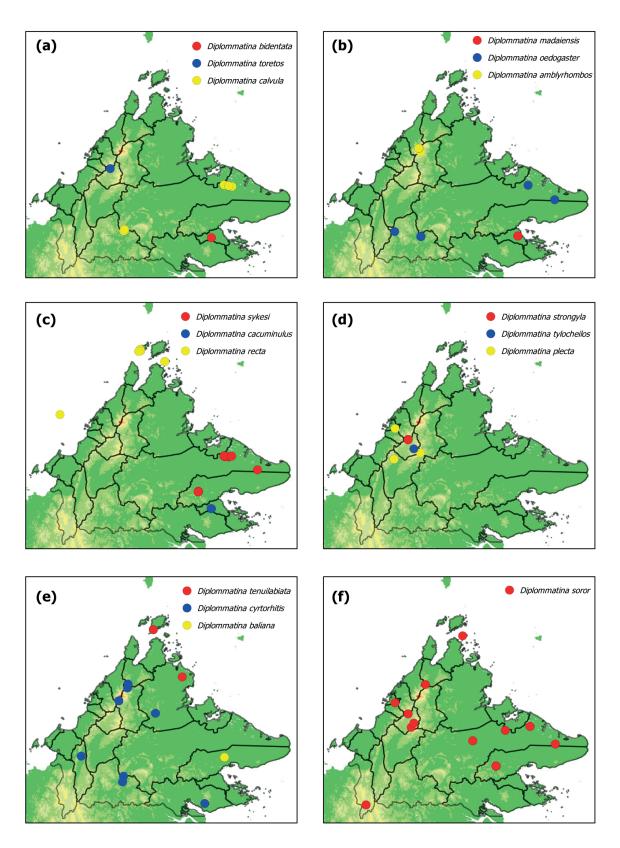


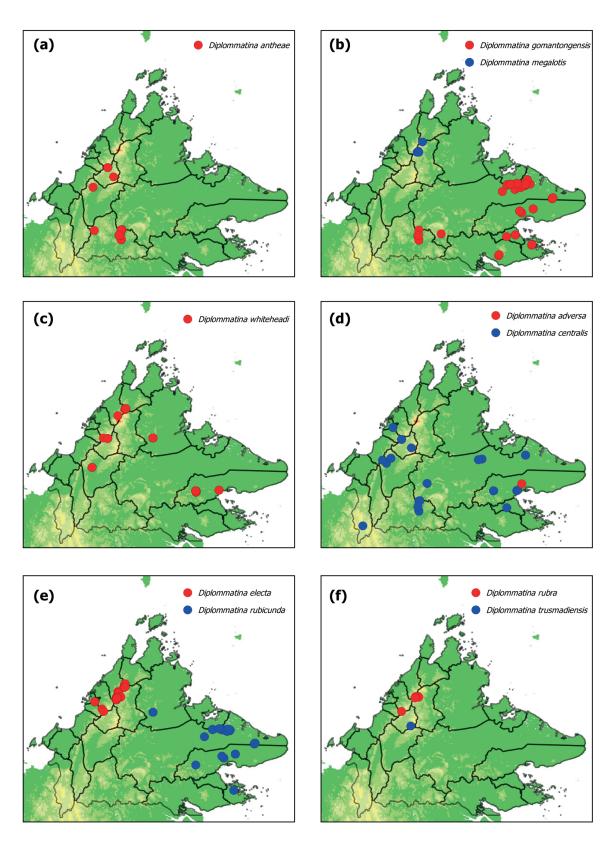




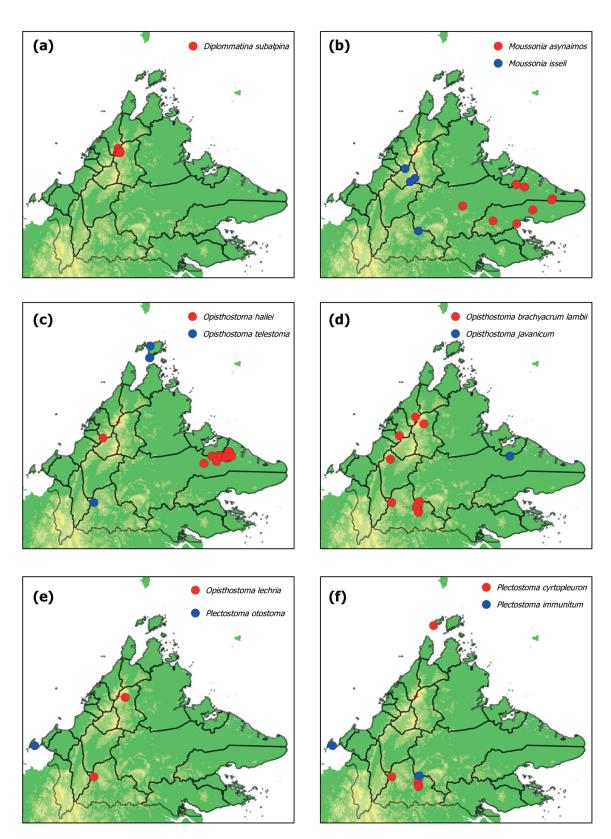


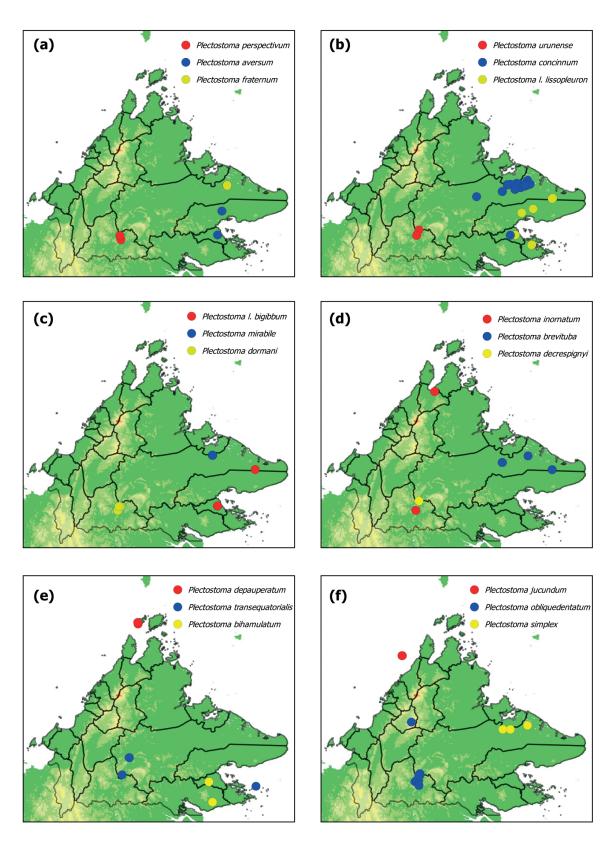




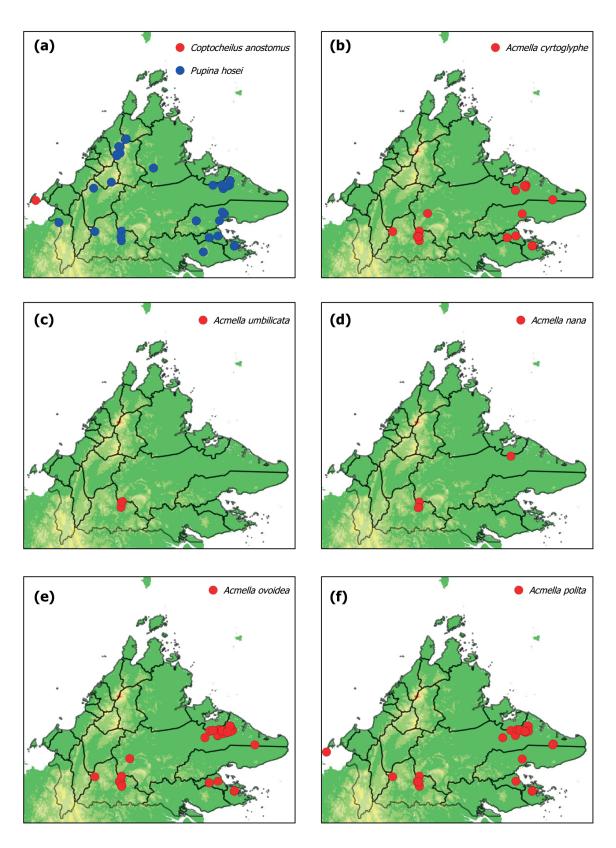


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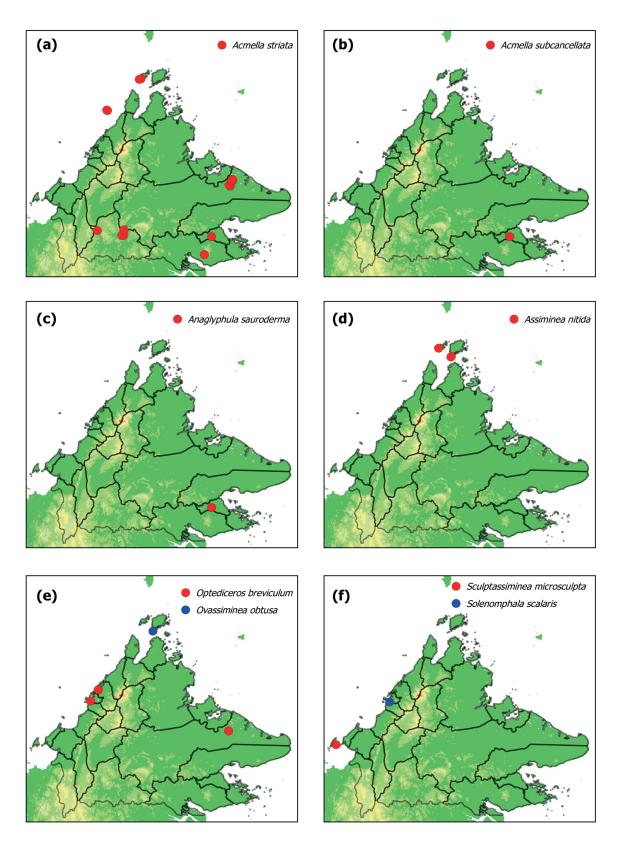




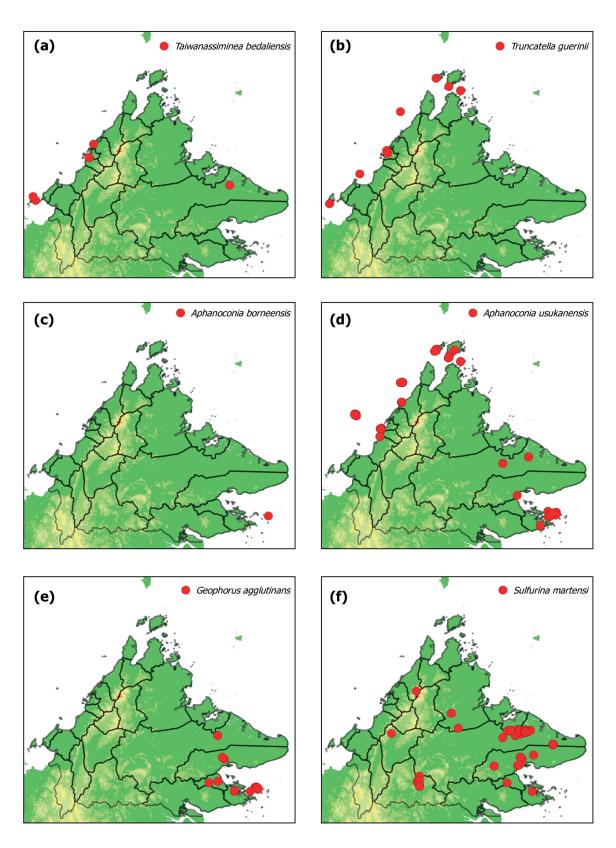
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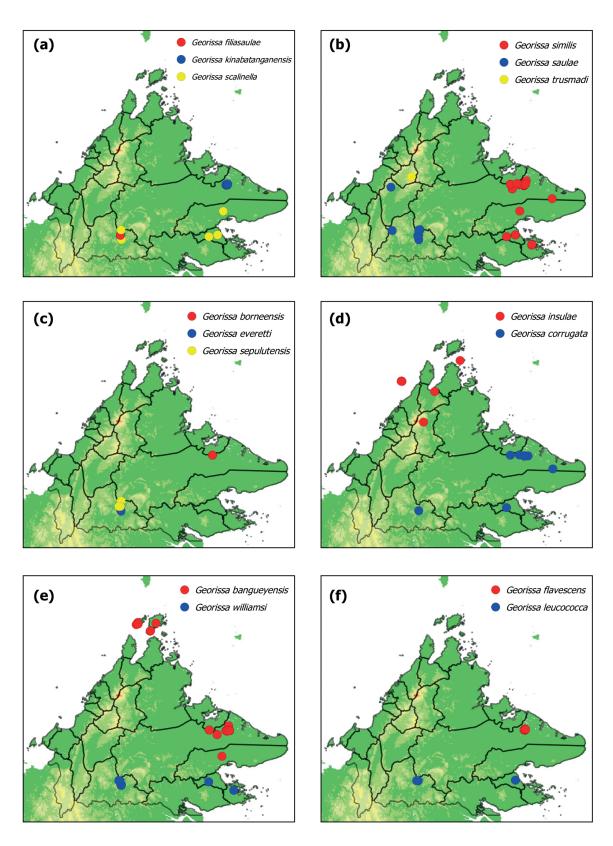
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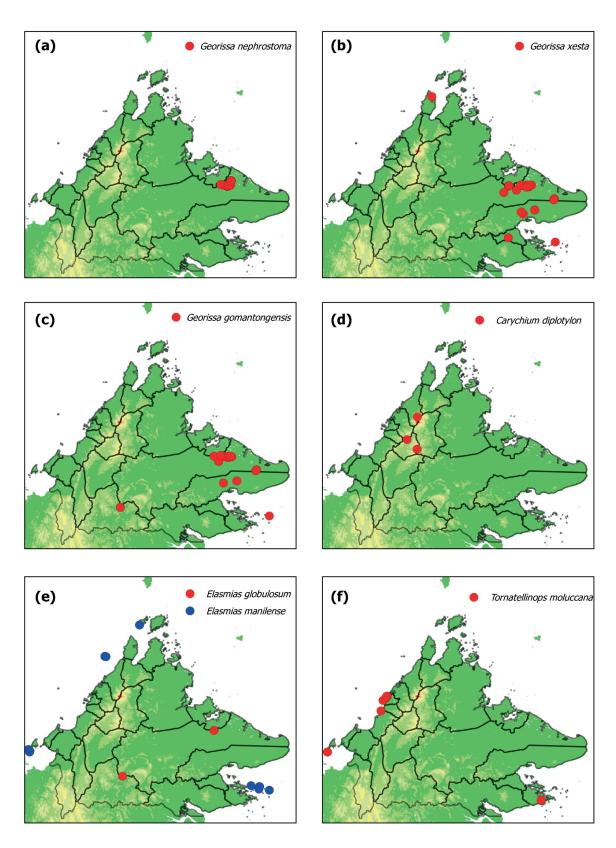
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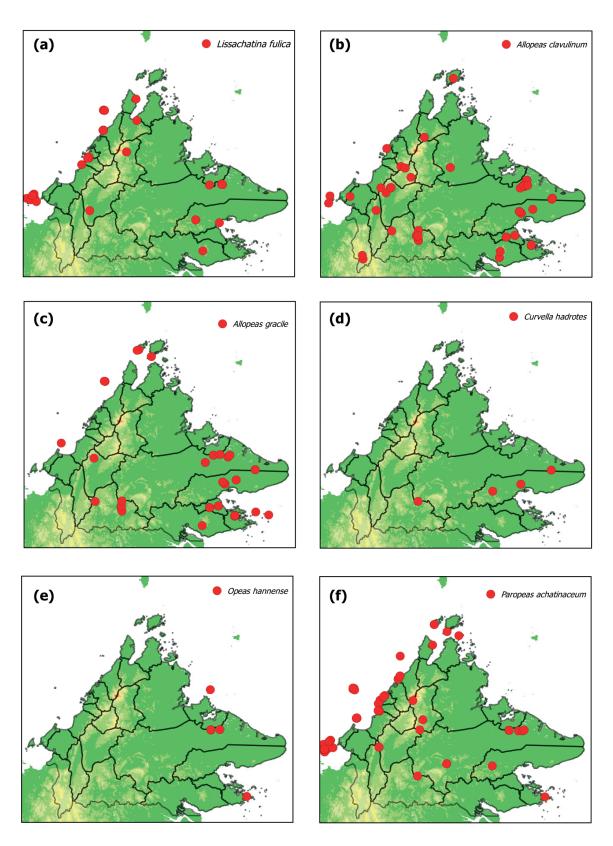
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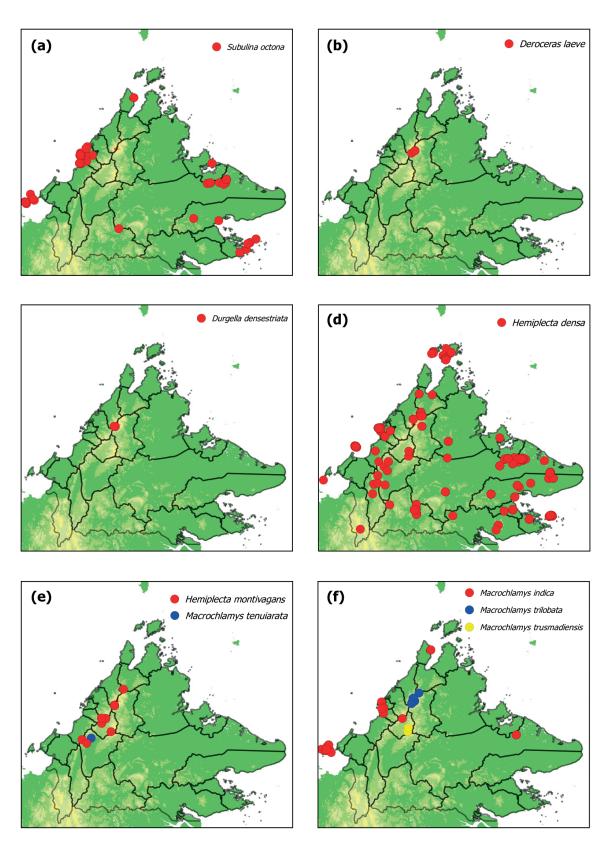
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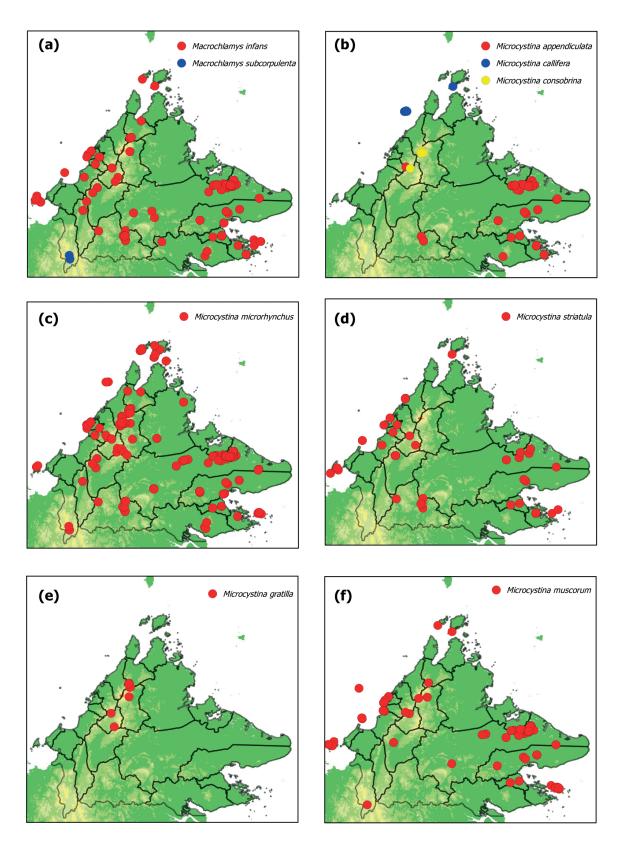


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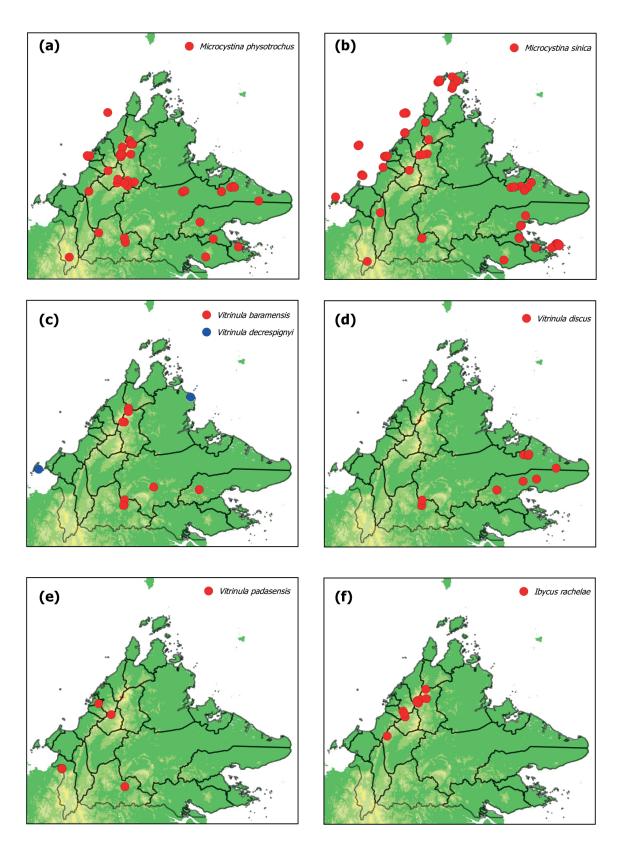


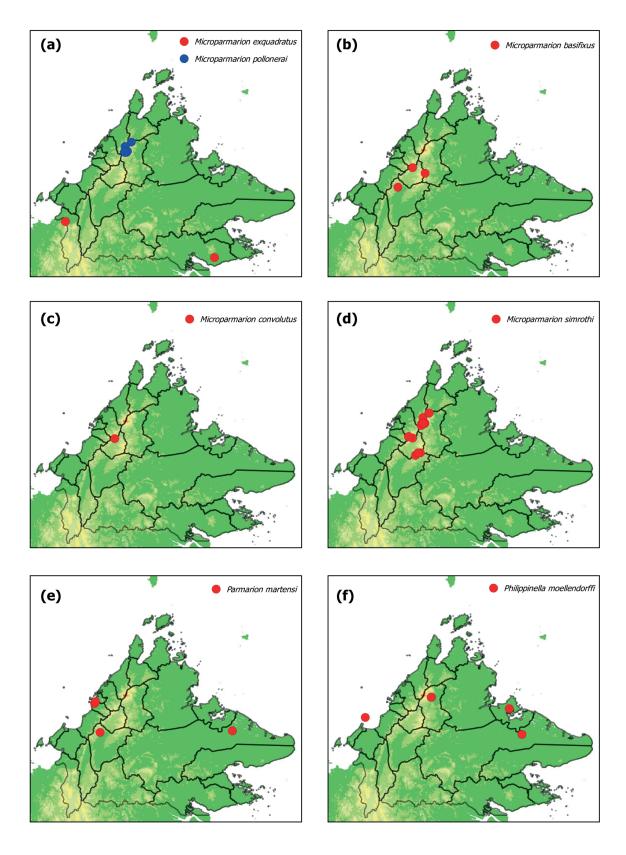
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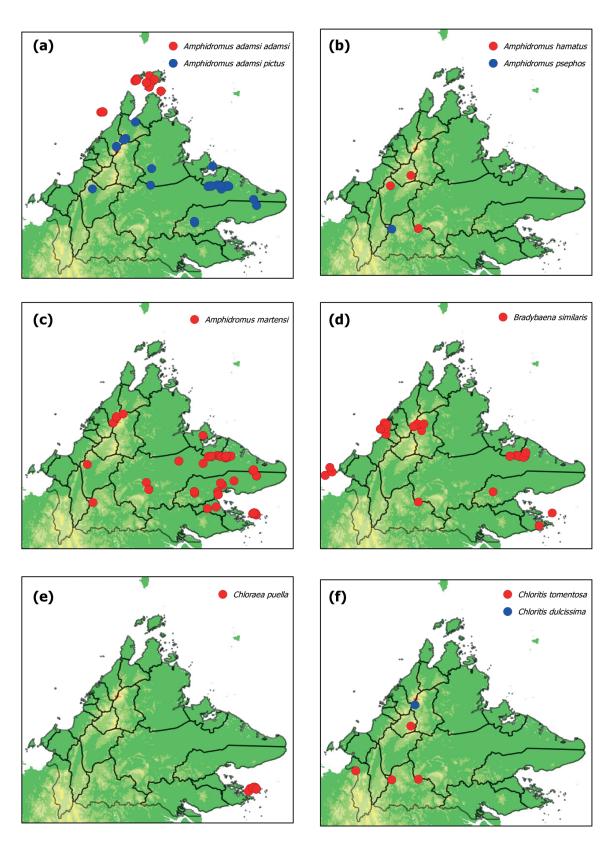




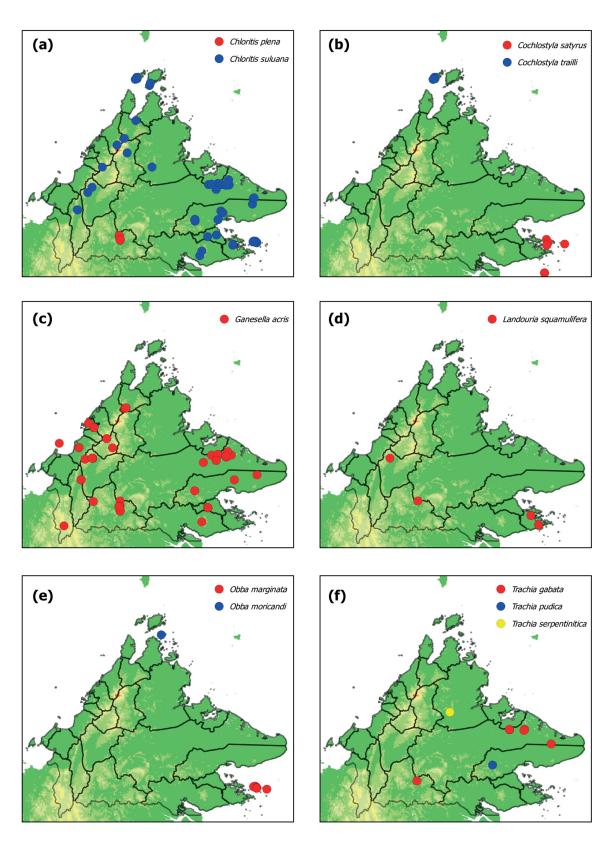
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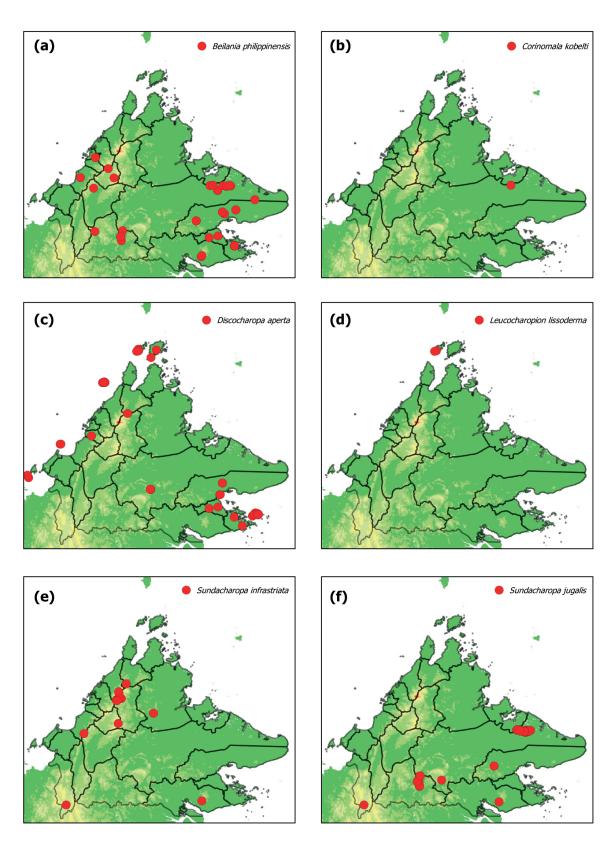




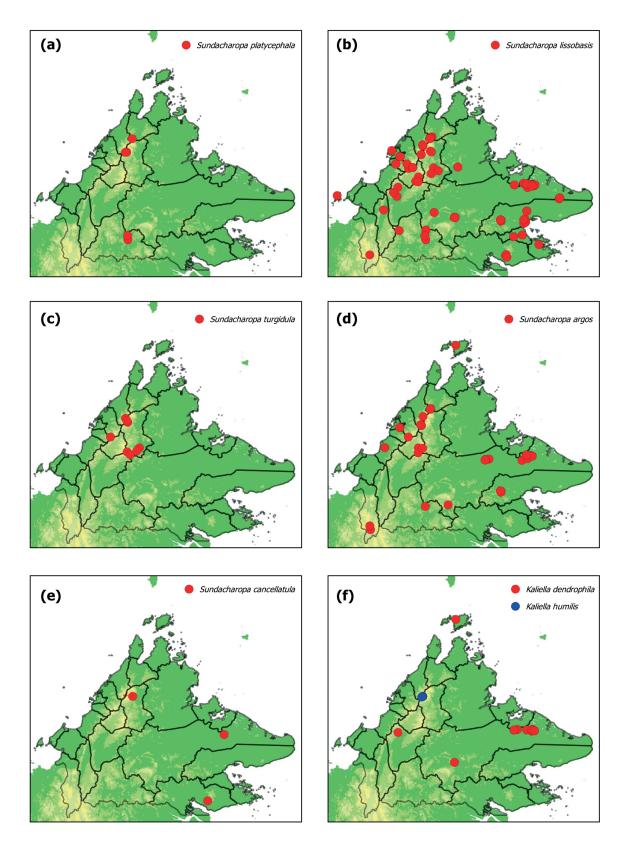
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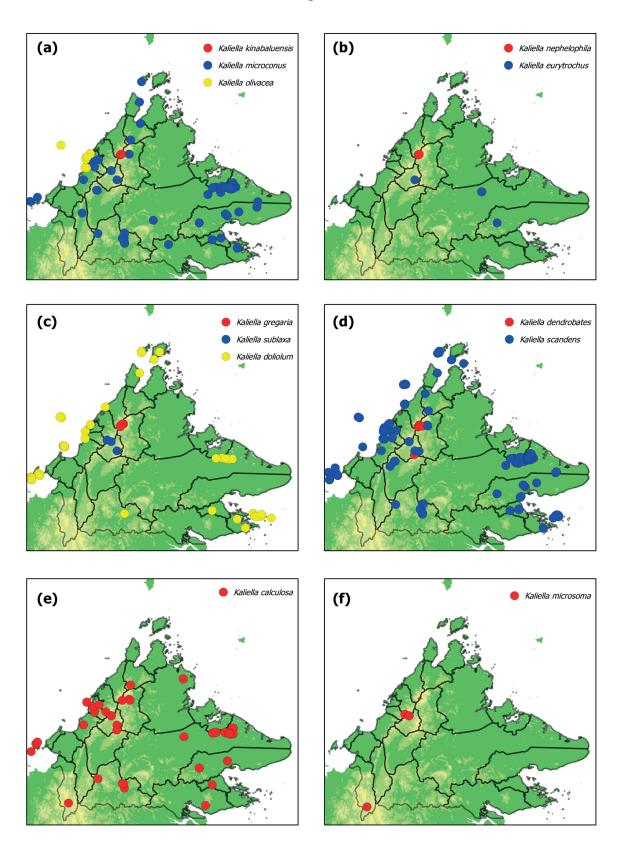
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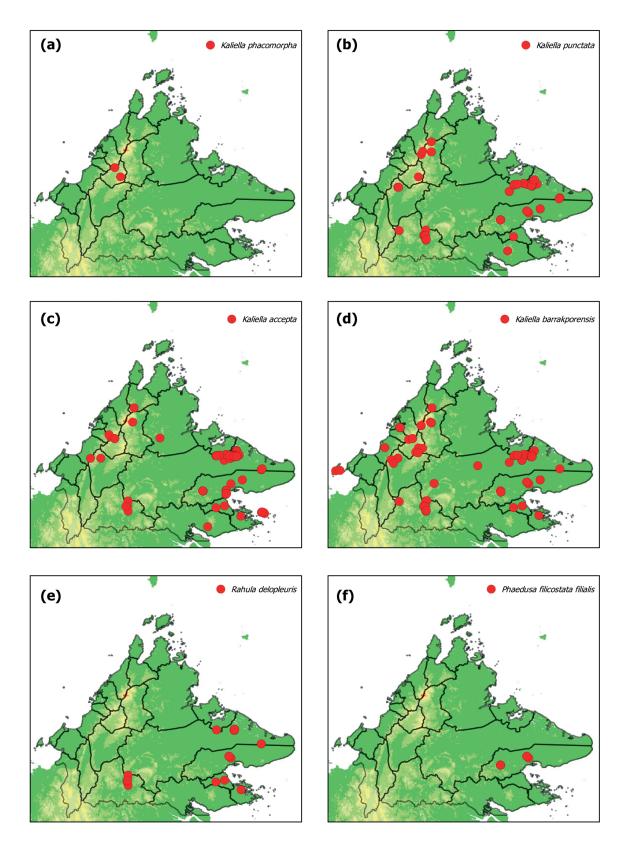
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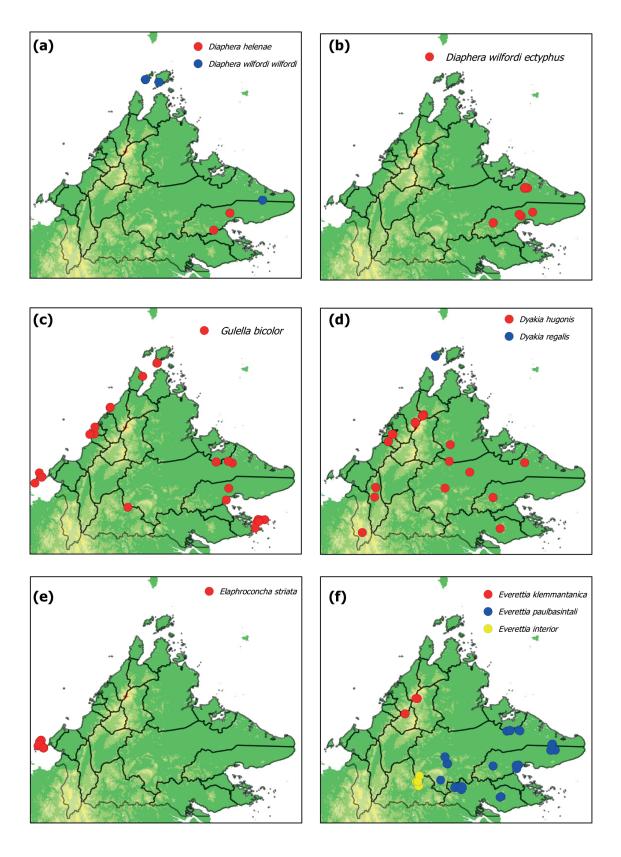
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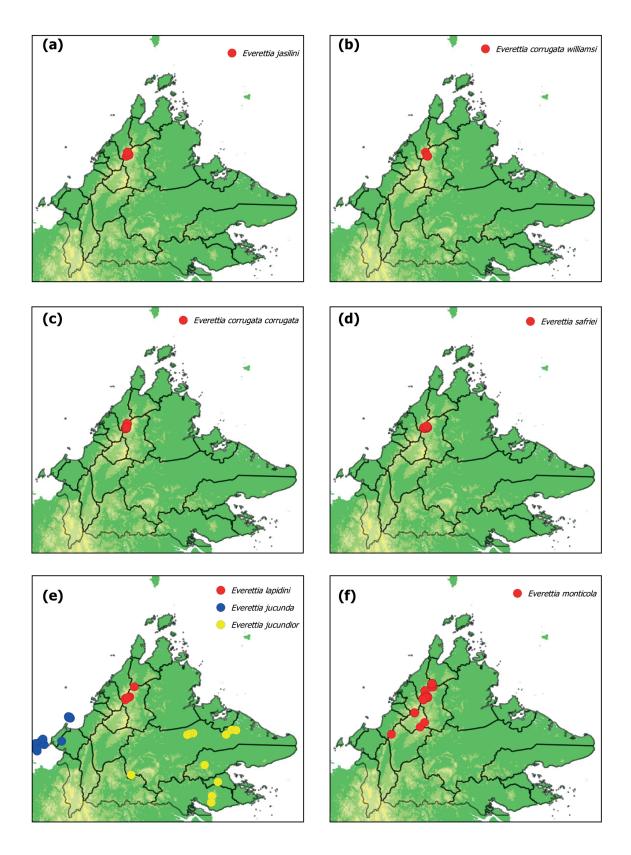
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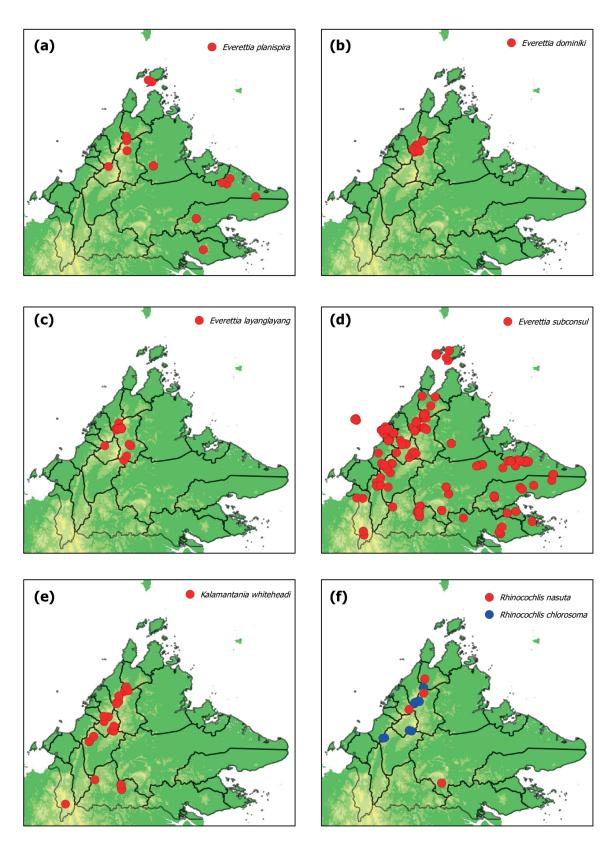
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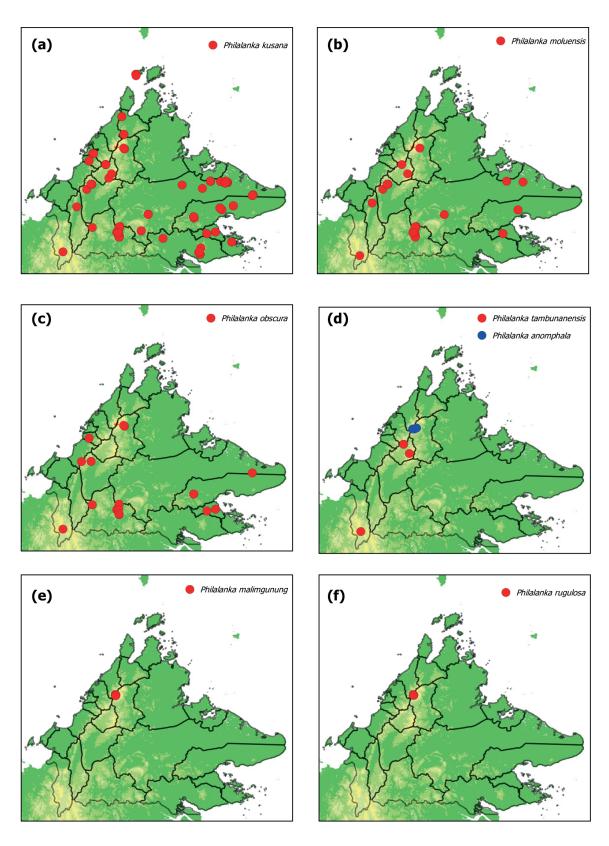
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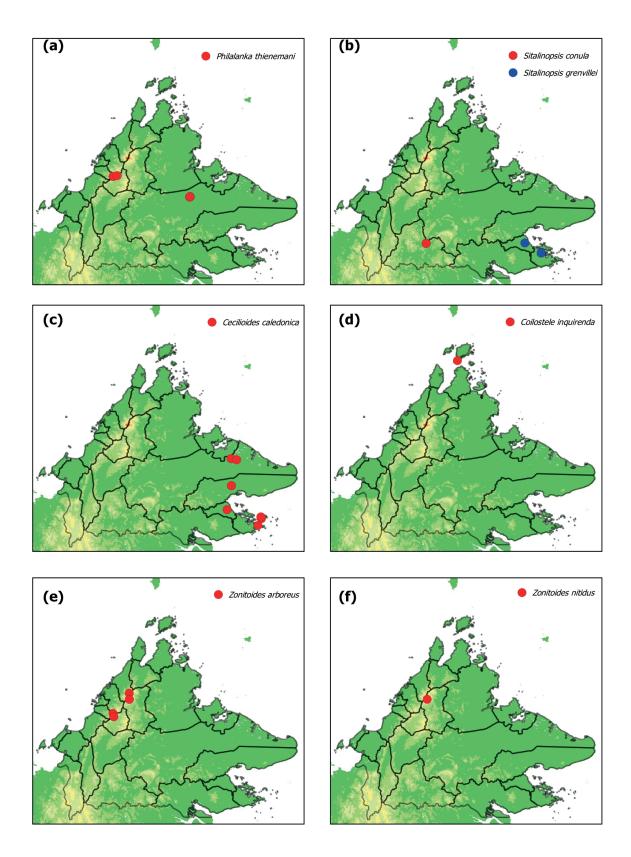
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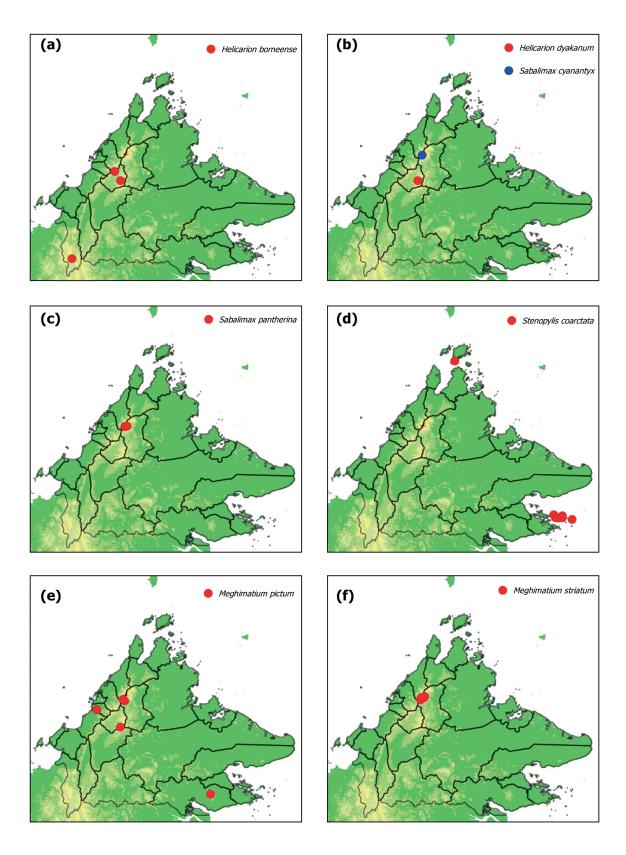
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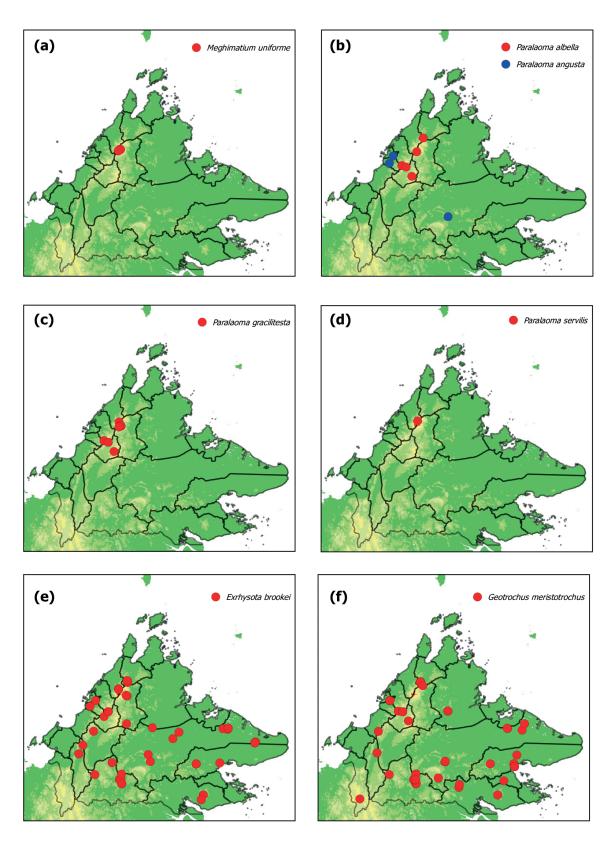
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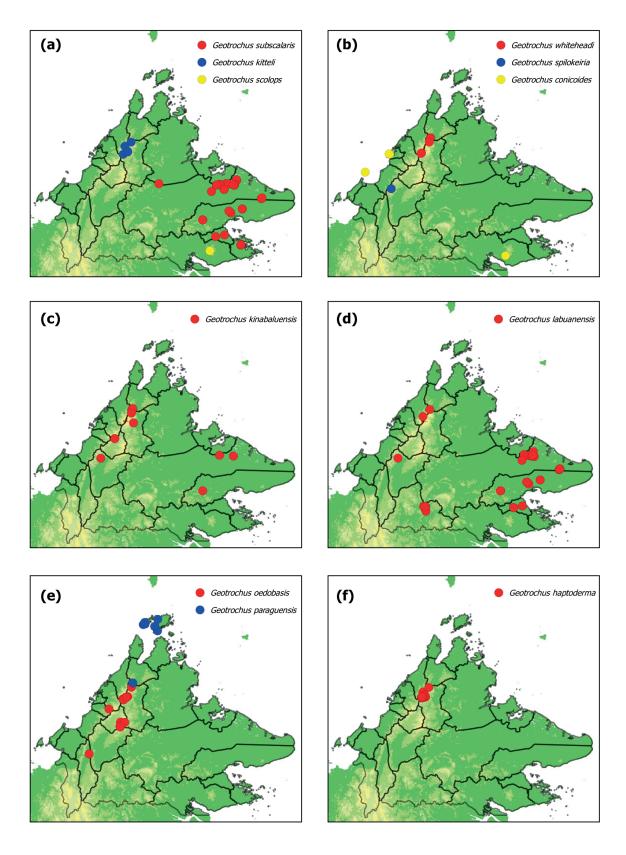
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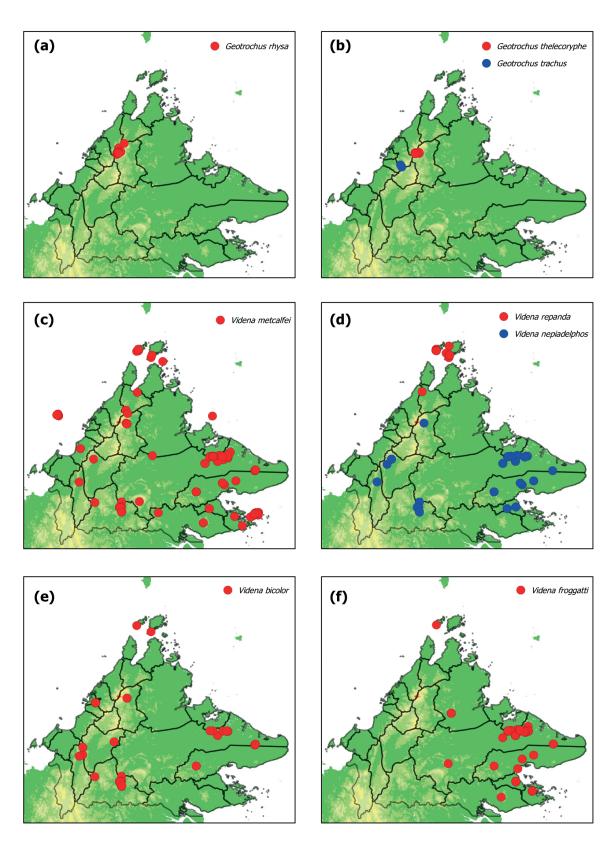
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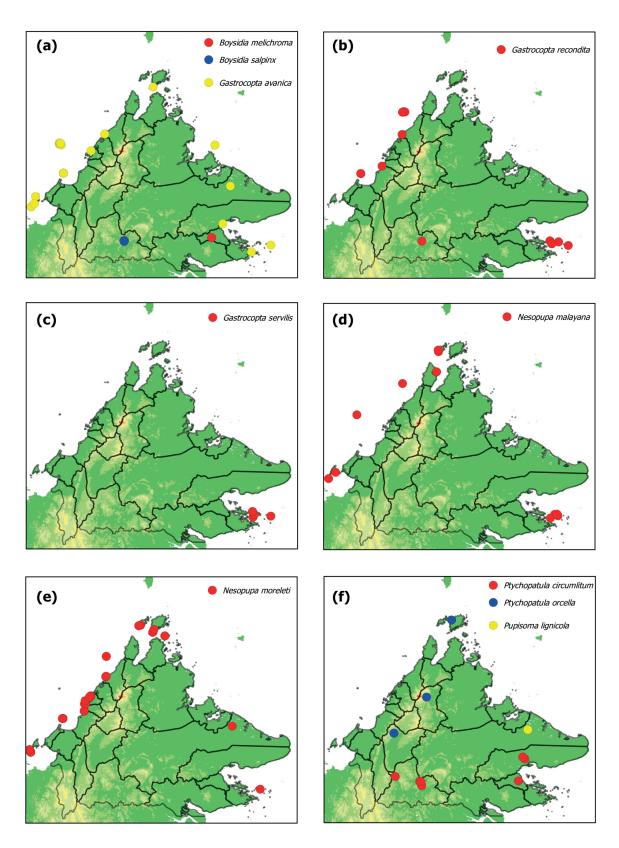
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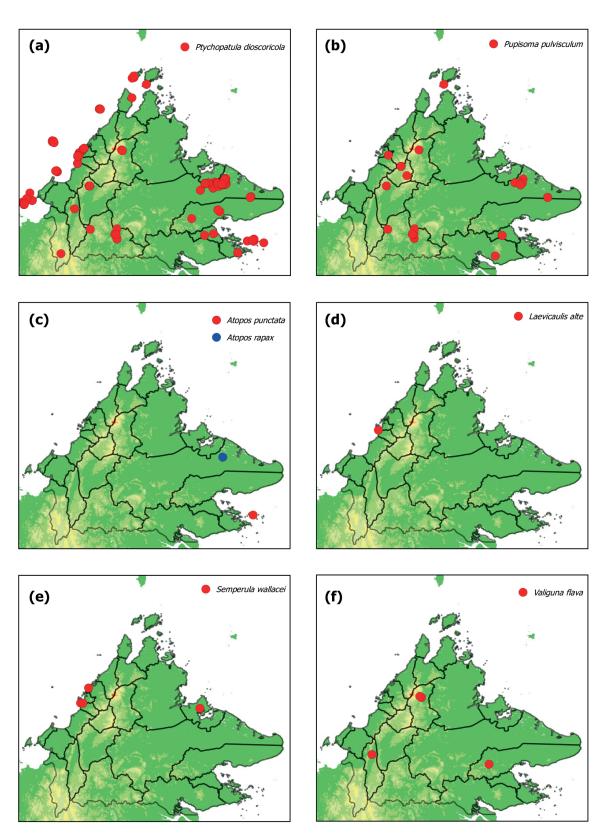
Map 36



Map 37



Map 38



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Additional information with illustrations

- Fig. 14, a-b. Malaysia, Sabah, Sukau. Photos: T-S Liew.
- Fig. 15, a–c. Malaysia, Sabah, lower Segama river valley, Sabahmas cave (JV 17647, paratype); d–f. Malaysia, Sabah, Kinabatangan river valley, Batu Keruak (JV 9810); g–h. Malaysia, Sabah, lower Segama river valley, Tabin river (JV 7748); i–l. Malaysia, Sabah, Sepulut valley, Gua Pungiton (JV 7530, paratype).
- Fig. 16, a-c. Malaysia, Sabah, mount Trusmadi (JV 13230); d-f. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (JV 1700).
- Fig. 17, a. Malaysia, Sabah, Sepulut area; b. Malaysia, Sarawak, Bukit Sarang (JV 12771). Photos: a. T-S Liew; b. J J Vermeulen.
- Fig. 18, a-b. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 1593); c-d. Malaysia, Sarawak, Niah Caves N.P. (JV 1580); e-f. Malaysia, Sarawak, Bau area, gunung Kapur (JV 2044); g. Malaysia, Sarawak, Bau area, Kampong Beratok (JV 2000).
- Fig. 19, a-b. Malaysia, Sabah, upper Padas river valley, near Long Pasia (NNM 5003917, holotype).
- Fig. 20, a–b. Malaysia, Sabah, Sepulut valley, Gua Sanaron (NNM 5003919, holotype); c–e. Malaysia, Sabah, Danum Valley Conservation Area (JV 9881); f–g. Malaysia, Sabah, Crocker Range N.P. above Tambunan (NNM 5003918, holotype, shell partly reconstructed); h. Malaysia, Sabah, Kinabalu N.P. (BOR/MOL 4118); i. Indonesia, Kalimantan Selatan, Meratus mountains (JV 3003); j–k. Malaysia, Sabah, Danum Valley Conservation Area (NNM 5003920, holotype).
- Fig. 21, a-b. Indonesia, Kalimantan Timur, Sangkulirang Peninsula (NNM 5003921, holotype); c-d. Malaysia, Sarawak, Bau area (JV 2621, shell partly reconstructed).
- Fig. 22, a. Malaysia, Sabah, Kinabalu N.P. (BOR/MOL 4086); b. Malaysia, Sabah, Kinabalu N.P. (BOR/MOL 14185); c. Malaysia, Sabah, mount Trusmadi (BOR/MOL 1608). Photos: T-S Liew.
- Fig. 23, a-b. Malaysia, Sabah, Kinabalu N.P. (JV 14497); c-d. Malaysia, Sabah, mount Trusmadi, Gua Dawaras (JV 14345, paratype).
- Fig. 24, a–c. Malaysia, Sabah, Crocker Range N.P., Gua Laing (NNM 5003957, holotype); d–f. Malaysia, Sarawak, Batu Niah (JV 1542); g–i. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 1596); j–k. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9536, paratype).
- Fig. 25, a–c. Malaysia, Sabah, Kinabalu N.P., mount Tambuyukon, near Monggis-Tambuyukon trail (BOR/MOL 14195, holotype); d–f. Malaysia, Sarawak, Gunung Mulu N.P. (JV 2673); g. Malaysia, Sabah, Crocker Range N.P., Gua Laing (JV 1125); h–k. Malaysia, Sabah, Banggi island, Karakit hill (JV 1443, paratype).
- Fig. 26, a–b. Malaysia, Sabah, mount Trusmadi, Gua Loloposon (BOR/MOL 14838, holotype); c–e. Malaysia, Sabah, Banggi island (JV 5594); f. Malaysia, Sabah, Bukit Pababola near Semporna (JV 1573); g–i. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (JV 1709).
- Fig. 27, a-b. Malaysia, Sabah, Banggi island (JV 1444); c-d. Malaysia, Sabah, Balambangan island, Batu Sireh (JV 9561). Photos: J J Vermeulen.
- Fig. 28, a–b. Malaysia, Sabah, Banggi island (JV 1444); c–f. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 1664); g–i. Indonesia, Kalimantan Timur, Gunung Siamang, Desah Liu c. 30 km east of Tandjung (HNHM 104883, holotype).
- Fig. 29, a-d. Malaysia, Sarawak, Batu Niah (JV 1541); e-f. Malaysia, Sabah, Danum Valley Conservation Area (JV 13475); g-i. Malaysia, Sabah, 'Kirk's Cave' near Lahad Datu (JV 2521).
- Fig. 30, a. Malaysia, Sabah, Kinabalu N.P.; b. Malaysia, Sabah, mount Trusmadi, 2350 m alt.; c. Malaysia, Sabah, Silam Coast Conservation Area; d. Malaysia, Sabah, Sukau; e. Malaysia, Sabah, Kinabalu N.P.; f. Malaysia, Sabah, Sugut; g. Malaysia, Sabah, Semporna; h Indonesia, Kalimantan Timur (JV 12352). Photos: a–g. T-S Liew; h. J J Vermeulen.
- Fig. 31, a–c. Malaysia, Sabah (NNM); d–e. Malaysia, Sabah, Semporna Islands Park, Pulau Bod Gaya (BOR/MOL 3538); f–g. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 1651); h–i. Malaysia, Sarawak, Batu Niah (JV 1536); j. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (JV 1710).
- Fig. 32, a-d. Malaysia, Sabah, lower Kinabatangan river valley, Tandu Batu (JV 9632); e-h. Indonesia, Kaliman-

- tan Timur, Kutei N.P. (JV 4522).
- Fig. 33, a–c. Malaysia, Sabah, Semporna area, Batu Tengar (JV 1799); d–e. Malaysia, Sabah, Balambangan island, Batu Sireh (JV 9561).
- Fig. 34, a–c. Malaysia, Sabah, Pun Batu (JV 1313); d. Malaysia, Sabah, Crocker Range N.P., Mahua falls (JV 9722); e–h. Malaysia, Sabah, Sepulut valley, Gua Sanaron (JV 7654); i–l. Malaysia, Sabah, Kinabalu N.P. (JV 4801).
- Fig. 35, a–c. Malaysia, Sabah, Pinangah river valley, Batu Urun (BOR/MOL 14846, holotype); d–f. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 7790); g–i. Malaysia, Sabah, Meliau range, east of Solonsong river, north of Telupid (BOR/MOL 14847, holotype).
- Fig. 36, a. Malaysia, Sabah, Tawau Hills N.P., bukit Bombalai (JV 13162); b. Malaysia, Sabah, Sukau; c. Malaysia, Sabah, Lumaku; d. Malaysia, Sabah, Kinabalu N.P., mount Tambuyukon; e. Malaysia, Sabah, locality unknown; f. Malaysia, Sabah, Tawau Hills N.P., Bukit Bombalai (JV 13170). Photos: a. J J Vermeulen; b–f. T-S Liew.
- Fig. 38, a–c. Malaysia, Sabah, Banggi island (a. NNM 57208, holotype; b–c. JV 1449); d–f. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (d. NNM 57209, holotype; e–f. JV 1586); g. Malaysia, Sabah, Kinabatangan river valley, along road Sandakan to Lahad Datu, near Kinabatangan river (UF 236672, holotype); h–j. Malaysia, Sarawak, Gunung Mulu N.P. (h. NNM 57210, holotype; i–j. JV 2670).
- Fig. 39, a–d. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (a. NNM 57211, holotype; b–d. JV 1585); e–g. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 1587); h. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 4563); i–k. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (i. NNM 57212, holotype; j–k. JV 1708).
- Fig. 40, a–c. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (a. NNM 57223, holotype; b–c. JV 1836, paratypes); d–f. Malaysia, Sabah, Pulau Tiga in Kimanis bay (JV 11351, paratype); g–i. Sabah, Sepulut valley, hill 1 km SE of Simatuoh (g. UF 196700, holotype; h–i. UF 196700, paratype); j–l. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (j. NNM 57217, holotype; k–l. JV 4560, paratype).
- Fig. 41, a–c. Malaysia, Sarawak, bukit Vrong near Beluru (a. UF 236655, holotype; b–c. UF 236655, paratypes); d–f. Indonesia, Kalimantan Timur, gunung Melihat (JV 2943); g–h. Malaysia, Sarawak, Gunung Mulu N.P. (g. NNM 57221, holotype; h. JV 2672, paratype); i. Malaysia, Sarawak, Bukit Sarang (UF 236659); j–l. Indonesia, Kalimantan Timur, gunung Melihat (j. NNM 57222, holotype; k–l. JV 2944, paratypes); m. Indonesia, Kalimantan Selatan, Jaro near Muara Uja (JV 3202).
- Fig. 42, a, c–d. Malaysia, Sabah, Batu Tengar near Semporna (a. NNM 57216, holotype; c–d. JV 1806); b. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 4561).
- Fig. 43, a–b. Malaysia, Sabah, Sepulut valley, hill 1 km SE of Simatuoh (UF 196504, holotype); c. Malaysia, Sabah, 'Kirk's Cave' near Lahad Datu (NNM 57226, holotype); d–f. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (d. NNM 57224, holotype; e–f. JV 11668, paratypes); g–k. Malaysia, Sabah, Semporna area, Bukit Pababola (g, i–k. JV 1702, paratypes; h. NNM 57225, holotype).
- Fig. 44, a-b. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (NNM 5003954, holotype); c-f. Malaysia, Sarawak, Bau area, gunung Pangga (c-e. NNM 56714, holotype; f. JV 2138, paratype).
- Fig. 45, a–c. Malaysia, Sabah, Pun Batu (NNM 56718, holotype); d–f. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (NNM 56716, holotype); g–i. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (SMF 192580, holotype); j–k. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (NNM).
- Fig. 46, a–c. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (NNM 56721, holotype); d–f. Malaysia, Sabah, mount Kinabalu (NHMUK 94.7.20.79–80, syntype); g–i. Malaysia, Sarawak, Batu Niah (NNM 56719, holotype); j–k. Malaysia, Sabah, mount Trusmadi (NNM 5003953, holotype).
- Fig. 47, a. Malaysia, Sabah, Kinabalu N.P., near Kotal route (BOR/MOL 14791, holotype); b, e. Malaysia, Sabah, Kinabalu N.P., near Sayap-Nunuhon trail (BOR/MOL 4224, paratype); c, d. Malaysia, Sabah, Kinabalu N.P., near Kotal route (BOR/MOL 4221, paratype); f–h. Malaysia, Sabah, mount Kinabalu (NHMUK 1901.12.9.106, holotype); i–k. Malaysia, Sabah, Pulau Banggi (SMF 105167, paratype).
- Fig. 48, a–c. Malaysia, Sabah, Pinangah river valley, Batu Urun (NNM 56715, holotype); d–e. Indonesia, Bali (VK 16008); f–h. Malaysia, Sarawak, bukit Vrong near Beluru (UF 193432, holotype).
- Fig. 49, a-c. Malaysia, Sabah, Crocker Range N.P., Laing Cave (NNM 56713, holotype); d-f. Malaysia, Sabah,

- Baturong-Madai F.R., Batu Baturong (JV 1833).
- Fig. 50, a-b. Malaysia, Sabah, Sukau. Photos: T-S Liew.
- Fig. 51, a-b. Malaysia, Sabah, Crocker Range N.P. (JV 1184); c-e. Malaysia, Sarawak, Bau area, gunung Kapur (JV 2237); f-h. Malaysia, Sabah, Batu Punggul (NNM 56723, holotype).
- Fig. 52, a–c. Malaysia, Sabah, Kinabalu N.P. (JV 1194); d–f. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 1672); g–i. Malaysia, Sabah, Kinabalu N.P. (JV 1439).
- Fig. 53, a–c. Malaysia, Sabah, Kinabalu N.P., near Kotal route (BOR/MOL 14733, holotype); d–f. Malaysia, Sabah, mount Trusmadi, Gua Dawaras (BOR/MOL 14837, holotype); g–i. Malaysia, Sabah, Kinabalu N.P., near Kotal route (JV 14321, paratype).
- Fig. 54, a–c. Malaysia, Sarawak, Limbang river valley (UF 193489, holotype); d–f. Malaysia, Sabah, Pinangah river valley, Batu Urun (JV 1149).
- Fig. 55, a–c. Malaysia, Sabah, Pun Batu (a, c. NNM 56590, holotype; b. JV 1290, paratype); d–e. Malaysia, Sabah, Kinabatangan river valley, Agop Batu Tulug (JV 1475).
- Fig. 56, a–b. Malaysia, Sabah, Crocker Range N.P., Laing cave (a. NNM 56595, holotype of O. lambii; b. JV 1113, paratype); c–d. Malaysia, Sarawak, Bau area, gunung Jambusan (JV 2097, paratypes of O. tarphypleura); e–f. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (NNM 56596, holotype of O. aetheroscopa); g. Indonesia, Kalimantan Timur (JV 2498); h. Malaysia, Sabah, Pun Batu (NNM 56599, holotype).
- Fig. 57, a, c, f. Malaysia, Sabah, Pun Batu (a. NNM 56923, holotype; c, f. JV 1285, paratypes); b, d, e. Malaysia, Sabah, Batu Punggul (JV 1892); g–h. Malaysia, Sabah, Pinangah valley, Batu Urun (BOR/MOL 14844, holotype); i–j. Malaysia, Sabah, Pinangah valley, Batu Urun (JV 18105, paratype).
- Fig. 58, a–c. Malaysia, Sabah, Batu Punggul (NNM 56921, holotype); d–g. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (d–f. BOR/MOL 14843, holotype; g. JV 7691, paratype).
- Fig. 59, a-d. 'N Borneo' (UF 133015); e-f. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (NNM); g-h. Malaysia, Kinabatangan river valley, Agop Batu Tulug (JV 1473).
- Fig. 60, a-d. Malaysia, Sabah, Semporna area, Bukit Pababola (a-b. NNM 56919, holotype, c-d. JV 1702, paratypes); e-g. Malaysia, Sabah, 'Kirk's Cave' near Lahad Datu (JV 1252).
- Fig. 61, a-e. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (a-b. NNM 56920, holotype, c-e. JV 1702, paratypes).
- Fig. 62, 8 a-d. Malaysia, Sabah, Kinabatangan river valley, Bukit Gomantong (JV 1592); e. Malaysia, Sabah, Kinabatangan river valley, Suanlamba (UF 194816).
- Fig. 63, a-h. Malaysia, Sabah, Sepulut valley, hill 1 km SE of Simatuoh (a, b. UF 196560, holotype, c-h. JV 13415, paratypes).
- Fig. 64, a–d. Malaysia, Sabah, Sepulut valley, hill 1 km SE of Simatuoh (a, b. UF 196684, holotype, c, d. JV 13413, paratypes); e–h. Malaysia, Sabah, 'small islands around Labuan' (NMW).
- Fig. 65, a–e. Malaysia, Sabah, Kinabatangan river valley, Agop Batu Tulug (a, b. NNM 56929, holotype, c–e. JV 1472, paratypes); f–h. Malaysia, 'N Borneo' (f, g. NNM, h. UF 160188).
- Fig. 66, a–d. Malaysia, Sarawak, Limbang river valley, gunung Budah near Medalam river (UF 194834); e, f, i. Indonesia, Kalimantan Selatan, gunung Buleh near Murara Uja; (e. NNM 56918, holotype, f, i. JV 3699, paratypes); g, h, j. Indonesia, Kalimantan Timur, gunung Melihat (JV 2947).
- Fig. 67, a–h. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (a, c. NNM 56917, holotype, b, d, e. JV 1837, paratypes, f–h. UF 196784); i–k. Malaysia, Sabah, Mantanani island (NMW).
- Fig. 68, a–e. Malaysia, Sabah, Sepulut valley, hill 4 km N of Simatuoh (a–b. UF 196726, holotype, c–e. JV 13414, paratypes); f–h. Malaysia, Kinabatangan river valley, Bukit Gomantong (JV 1589).
- Fig. 69, a. Malaysia, Sarawak, upper Kakus river valley (JV 12858); b. Malaysia, Sarawak, Gunung Mulu N.P., Deer Cave (JV 10530); c. Malaysia, Sarawak, Gunung Mulu N.P., along trail to Deer Cave and Lang's Cave (JV 4233). Photos: J J Vermeulen.
- Fig. 70, a. Malaysia, Sabah, Tawau Hills N.P., Bukit Bombalai; b. Malaysia, Sarawak, lower Tatau River valley, Bukit Sarang (JV 12855). Photos: J J Vermeulen.
- Fig. 71. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (JV 1701).

- Fig. 72, a–b. Malaysia, Sabah, Sepulut valley, Gua Sanaron (NNM 5003948, holotype); c–d. Malaysia, Sabah, Kinabatangan river valley, Batu Pangi (JV 9644); e–g. Malaysia, Sabah, Pinangah river valley, Batu Urun (e–f. NNM 5006946, holotype, g. JV 8016).
- Fig. 73, a–b. Malaysia, Sarawak, Niah Caves (NNM 5003950, holotype); c–d. Malaysia, Sabah, Pinangah river valley, Batu Urun (5003949, holotype); e–f. Malaysia, Sabah, Sepulut valley, Batu Temurung (JV 8019); g–h. Malaysia, Sabah, lower Segama river valley, Tabin river (JV 7762); i–j. Malaysia, Sabah, Balambangan island, Batu Sireh (NNM 5003947, holotype); k–l. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (NNM 9003945, holotype).
- Fig. 74, a-b. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (NNM 5003952, holotype).
- Fig. 75, a-b. Malaysia, Sabah, Labuan island, near Tanjung Aru (HR T2844); c-d. Malaysia, Sabah, Labuan island, near Tanjung Aru (HR T2846); e-f. Malaysia, Sabah, Labuan island, near Tanjung Aru (HR T2845). Photos: © J G M Raven.
- Fig. 76, a. Singapore, Pulau Semakau (JV 7400); b–c. Indonesia, Kalimantan Selatan, Pagatan (JV 3244); d. Brunei, Pantai Jerudong Beach (JV 10076); e–f. Malaysia, Sabah, Kota Kinabalu, Taman Happy Garden (BOR/MOL 14848); g–h. Malaysia, Sabah, kampong Sabandar (JV 12713).
- Fig. 77. Indonesia, Bali (JV 3352).
- Fig. 78, a–c. Malaysia, Sabah, Pulau Mataking off Semporna (JV 11522); d–e. Malaysia, Sabah Balambangan island, Batu Sireh (JV 9562); f. Malaysia, Sabah, Batu Tengar near Semporna (JV 1792); g. Sabah, lower Segama river valley, Tabin river (JV 7737); h. Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak (JV 9804).
- Fig. 79, a. Malaysia, Sabah, Manukan island; b. Malaysia, Sabah, Sukau. Photos: T-S Liew.
- Fig. 80, a–d. Malaysia, Sabah, Sepulut valley, Gua Pungiton (BOR/MOL 12768); e–h. Malaysia, Sabah Sepulut valley, Gua Sanaron (BOR/MOL 3493); i–l. Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak (MZU/MOL 17.26). SEM-images: © M Z Khalik.
- Fig. 81, a–d. Malaysia, Sabah, Teck Guan Cave ('Kirk's Cave') near Lahad Datu (ZMA/MOLL 135735); e–h. Malaysia, Sabah, Sepulut valley, Gua Pungiton (BOR/MOL 12278); i–l. Malaysia, Sabah, locality not given (ZMA/MOLL 315546). SEM-images: © M Z Khalik.
- Fig. 82, a–d. Malaysia, Sabah, Kinabatangan river valley, Batu Tomanggong (MZU/MOL 16.16); e–h. Malaysia, Sarawak, Niah Caves N.P. (JV 10185); i–l. Malaysia, Sabah, Bukit Gomantong (MZU/MOL 16.14). SEM-images: © M Z Khalik.
- Fig. 83, a–d. Malaysia, Sabah, mount Trusmadi, Gua Loloposon (MZU/MOL 16.18); e–h. Malaysia, Sabah, lower Kinabatangan river valley, Bukit Mawas (NNM 5004968); i–l. Malaysia, Sabah, lower Kinabatangan river valley, Batu Pangi (BOR/MOL 7288). SEM-images: © M Z Khalik.
- Fig. 84, a–d. Malaysia, Sarawak, Bau area, mount Rapih, (JV 12572); e–h. Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak (MZU/MOL 17/29); i–l. Malaysia, Sabah, lower Kinabatangan river valley, upper Resang river (BOR/MOL 7303). SEM-images: © M Z Khalik.
- Fig. 85, a–d. Malaysia, Sabah, Bukit Gomantong (BOR/MOL 7389); e–h. Malaysia, Sabah, Mantanani islands, Pulau Mantanani Besar (MZU/MOL 18.02); i–l. Malaysia, Sabah, Sepulut area, Simbaluyon hill (NNM 333946). SEM-images: © M Z Khalik.
- Fig. 86. Malaysia, Sabah, Crocker Range N.P., Mahua falls (JV 9731, paratype).
- Fig. 87, a. Malaysia, Sabah, Pinangah river valley, Batu Urun (JV 1174); b. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9526); c–d. Malaysia, Sabah, Mantanani islands, Pulau Mantanani Besar (JV 9839); e. Malaysia, Sabah, Semporna area, Bukit Tengkorak (JV 12737).
- Fig. 88. Malaysia, Sabah, Baturong-Madai F.R., Bukit Madai (V).
- Fig. 89, a–b. Indonesia, Bali (JV 3494); c–d. Indonesia, Java, Nusa Penida (JV 4369); e–f. Malaysia, Sabah, Danum Valley Conservation Area (BOR/MOL 663, holotype); g. Indonesia, Sulawesi Utara, Bolaang Mongondow (JV 1072); h. Malaysia, Sarawak, Bau area (JV 12686); i–j. Indonesia, Java, Nusa Penida (JV 4094).
- Fig. 90, a. Malaysia, Sabah; b. Malaysia, Sabah, Kinabalu N.P. Headquarters area. Photos: T-S Liew.
- Fig. 91, a-c. Malaysia, Sabah, Kinabalu N.P. (BOR/MOL 6035, holotype, umbilical region reconstructed).
- Fig. 92, a-b. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (JV 7586); c-d. Malaysia, Sabah, Batu Pung-

- gul (JV 1990); e. Malaysia, Sabah, lower Segama river valley, Tabin river (JV 7788); f-h. Malaysia, Sabah, Kinabalu N.P. (JV 4798); i. Malaysia, Sabah, mount Trusmadi, Forestry chalet (JV 13210, paratype). Photos: J J Vermeulen.
- Fig. 93, a. Origin unknown (After sketch of T-S Liew); b. Malaysia, Sabah, Kinabalu N.P. (After Liew et al. 2009).
- Fig. 94, a–c. Singapore, near Bukit Timah N.P. (JV 7922); d–f. Malaysia, Sabah, mount Trusmadi (JV 13225); g–i. Malaysia, Sabah, upper Padas river valley, tributary of Matang river, south of Long Pasia (BOR/MOL 14839, holotype).
- Fig. 95, a–d. Malaysia, Sabah, Crocker Range N.P., Gua Laing (a–c. BOR/MOL 15010, holotype; d. JV 1127, paratype); e–g. Malaysia, Sabah, mount Tambuyukon summit (BOR/MOL 14714, holotype); h–j. Malaysia, Sabah, mount Trusmadi (JV 13220).
- Fig. 96, a. Malaysia, Sabah, Kinabalu N.P., Layang Layang; b. Indonesia, Kalimantan Timur; c. Singapore (JV 13042); d. Malaysia, Sabah, Tawau Hills N.P., Bukit Bombalai (JV 13152); e. Malaysia, Sabah, mount Tambuyukon. Photos; f. Malaysia, Sarawak, Lanjak Entimau; g. Malaysia, Sarawak, Bukit Sarang (JV 12874); h. Malaysia, Sabah, Lumaku. Photos: b–d, f. J J Vermeulen; a, e, f, h. T-S Liew.
- Fig. 97, a–c. Malaysia, Sabah, Mantanani islands, Pulau Lungisan (NNM 5003934, holotype); d–f. Malaysia, Sabah, Sepulut valley, Gua Pungiton (NNM 5003933, holotype); g–i. Malaysia, Sabah, lower Segama river valley, Tabin river (NNM 5003935, holotype).
- Fig. 98, a-c. Malaysia, Sabah, lower Segama river valley, Tabin river (JV 7781); d-f. Indonesia, Sumatra (NNM, holotype); g. Malaysia, Sabah, Kinabalu N.P. (JV 14325); h-j. Indonesia, Java (NNM).
- Fig. 99, a–c. Indonesia, Bali (JV 3974); d–f. Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak (NNM 5003937, holotype); g–i. Malaysia, Sabah, Sepulut valley, Gua Sanaron (JV 8071); j. Indonesia, Kalimantan Selatan, Meratus mountains (JV 3061).
- Fig. 100, a. Malaysia, Sabah, Mantanani islands, Pulau Lungisan (BOR/MOL 3746); b. Malaysia, Sabah, Pulau Tiga in Kimanis bay (BOR/MOL 1100, lost); c. Material and data lost; d. Malaysia, Sabah, Kinabalu N.P., Kotal route (BOR/MOL 4003); e–f. Malaysia, Sabah, lower Kinabatangan river valley, Bukit Mawas (BOR/MOL 1341); g–h. Malaysia, Sabah, Kinabalu N.P., Monggis-Tambuyukon trail (BOR/MOL 4003). SEM-images: T-S Liew.
- Fig. 101, a–c. Indonesia, Kalimantan Timur, Sangkulirang peninsula (JV 12512); d–f. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 7505, paratype); g–h. Malaysia, Sarawak, Bukit Sarang (V11996); i–j. Malaysia, Sabah, Padas valley (NHMUK 1894.7.20.5-6, syntype, drawn from photographs).
- Fig. 102, a–d. Malaysia, Sabah, Crocker Range N.P., gunung Mas (JV 9875); e. Malaysia, Sabah, Tawau Hills N.P. (SP 13560, syntype, after Schilthuizen et al., 2019, modified); f–g. Malaysia, Sabah, mount Kinabalu (after Collinge & Godwin-Austen, 1895, modified).
- Fig. 103, a-b. Malaysia, Sabah, Crocker Range N.P., Ulu Kimanis (BOR/MOL 14840, holotype); c-f. Malaysia, Sabah, Crocker Range N.P., Mahua falls (JV 9725).
- Fig. 104, a–g. Malaysia, Sabah, Crocker Range N.P., Mahua falls (BOR/MOL 14841, holotype); h–i. Malaysia, Sabah, mount Kinabalu (after Collinge & Godwin-Austen, 1895, modified).
- Fig. 105, a–d. Malaysia, Sabah, Crocker Range N.P., Ulu Kimanis (JV 3211); e. Origin unknown (after Collinge & Godwin-Austen, 1895, modified); f–g. Philippines, Mindoro (after Collinge, 1899, modified).
- Fig. 106, a. Malaysia, Sabah, mount Trusmadi, 1900 m alt.; b. Malaysia, Sabah, Kinabalu N.P., Liwagu; c. Malaysia, Sabah, mount Lumaku; d. Malaysia, Sabah, Kinabalu N.P.; e. Malaysia, Sabah, Kinabalu N.P., Liwagu; f. Malaysia, Pahang, Kampong Merapoh. Photos: T-S Liew.
- Fig. 107, a. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9509); b. Malaysia, Sabah, Tawai mountains near Telupid (JV 1261); c. Malaysia, Sabah, mount Trusmadi (JV 13254); d–e. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (JV 1879); f. Malaysia, Sabah, Pun Batu near Sepulut (JV 1311, holotype).
- Fig. 108, a–b. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9509); c. Malaysia, Sabah, Tawai mountains near Telupid (JV 1261); d. Malaysia, Sabah, Mantanani Islands (JV 9838). Photos: J J Vermeulen.
- Fig. 109, a–e. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9509); f. Malaysia, Sabah, Tawai mountains near Telupid (JV 1261); g. Malaysia, Sabah, Mantanani Islands (JV 9838); h. Indonesia, Kalimantan Timur, Sangkulirang area (JV 12005). Photos: J J Vermeulen.

- Fig. 110, a–d. Malaysia, Sarawak, Gunung Mulu N.P. (JV 10575); e. Malaysia, Sabah, mount Trusmadi (JV 13254); f. Malaysia, Sabah, Pun Batu near Sepulut (JV 1311, paratype); g–h. Malaysia, Sabah, Semporna Islands Park, Pulau Bohay Dulang (JV 13537); i. Malaysia, Sabah, Bukit Gomantong (JV 1603); j–k. Malaysia, Sabah, Baturong-Madai F.R., Batu Baturong (JV 1879). Photos: J J Vermeulen.
- Fig. 111, a-b. Malaysia, Sabah, Pinangah river valley, Batu Urun (JV 1135); c-e. Malaysia, Sabah, Semporna Islands Park, Pulau Bohay Dulang (JV 13538); f-g. Malaysia, Sabah, mount Kinabalu (NHMUK 95.12.5.53).
- Fig. 112, a-b. Malaysia, Sabah, Batu Punggul (JV 1977); c. Malaysia, Sabah, 'Kirk's Cave' near Lahad Datu (JV 13354); d. Malaysia, Sabah, Tawau Hills N.P., Bukit Bombalai (JV 13166); e-f. Malaysia, Sabah, Pinangah river valley, Batu Urun (Bukit Sinobang) (JV 7999).
- Fig. 113, a-b. Malaysia, Sabah, Pulau Sipadan c. 40 km off Semporna (JV 4029); c. Malaysia, Sabah, Pulau Mataking off Semporna (JV 11511); d-e. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9505). Photos: J J Vermeulen.
- Fig. 114, a. Malaysia, Sabah, Pulau Mataking off Semporna (JV 11511); b. Malaysia, Sabah, Balambangan island, Kok Simpul (JV 9505); c–d. Malaysia, Sabah, Bukit Tengkorak near Semporna (JV 13535); e–f. Malaysia, Sarawak, Bau area (JV 5470).
- Fig. 115, a-b. Malaysia, Sabah, Semporna Islands Park, Pulau Bohay Dulang (JV 17640); c-e. Malaysia, Sabah, Malawati island (ZMA).
- Fig. 116, a–b. Malaysia, Sabah, lower Segama river valley, Tabin river (JV 7793); c–d. Malaysia, Sabah, Danum Valley Conservation Area (JV 17639); e–f. Malaysia, Sabah, gunung Meliau (BOR/MOL 3201, holotype).
- Fig. 117, a. Malaysia, Sarawak, Gunung Mulu N.P. (JV 10575); b. Malaysia, Sabah, Semporna; c. Malaysia, Sabah, Semporna; d. Malaysia, Sabah, Tun Sakaran Marine Park; e. Malaysia, Sabah, Semporna; f. Malaysia, Sabah, Balambangan island; g. Malaysia, Sarawak, Lanjak Entimau; h. Malaysia, Sabah, Semporna. Photos: a. J J Vermeulen; b–h. T-S Liew.
- Fig. 118, a–b. Malaysia, Sabah, lower Segama river valley, Sabahmas Cave (JV 7464); c–d. Malaysia, Sabah, Indonesia, Nusa Penida near Bali (JV 4102); e–f. Indonesia, Ambon (JV 5075); g–i. Indonesia, Kalimantan Selatan, Meratus mountains, west flank, Nateh near Bata Tangga, c. 18 km east of Barabai (HNHM 104884, holotype).
- Fig. 119, a–b. Malaysia, Sabah, upper Padas river valley, sandstone outcrops along tributary of Matang river, south of Long Pasia (JV 9921, paratype); c–d. Malaysia, Sabah, lower Kinabatangan river valley, Batu Keruak (JV 9793, paratype); e–f. Malaysia, Sabah, Kinabalu N.P., Mesilau trail (BOR/MOL 4146, holotype).
- Fig. 120, a–b. Malaysia, Sabah, Segama river valley, near bridge of road Sandakan to Lahad Datu (JV 7504, paratype); c–d. Malaysia, Sabah, Kinabalu N.P., Mesilau trail (BOR/MOL 4145, holotype, spire reconstructed); e–f. Malaysia, Sabah, upper Padas river valley, sandstone outcrops along tributary of Matang river, south of Long Pasia (JV 9818, paratype); g–h. Malaysia, Sabah, lower Kinabatangan river valley, Bukit Mawas (BOR/MOL 14836, holotype).
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Even specialists know the Bornean land snail fauna by the spectacular *Plectostoma* species only, but a reasonable estimate is that, eventually, the recorded Bornean snail fauna will pass a thousand different species.

Decades of collecting and research by the authors and others have made Sabah, Malaysia, the most thoroughly sampled and studied part of Borneo. In this book, all 343 species and subspecies of land snails and slugs currently known from Sabah, including the federal territory of Labuan, are revised and illustrated.

This book is an identification tool for students and specialists, for instance for those who use land snails as an indicator group for biodiversity assessments, to advise policymakers and planners on potential net loss of biodiversity because of development projects. Land snail species often occur restricted to a small area, especially on limestone hills, and development projects including limestone extraction can lead to the acute extinction of species.



